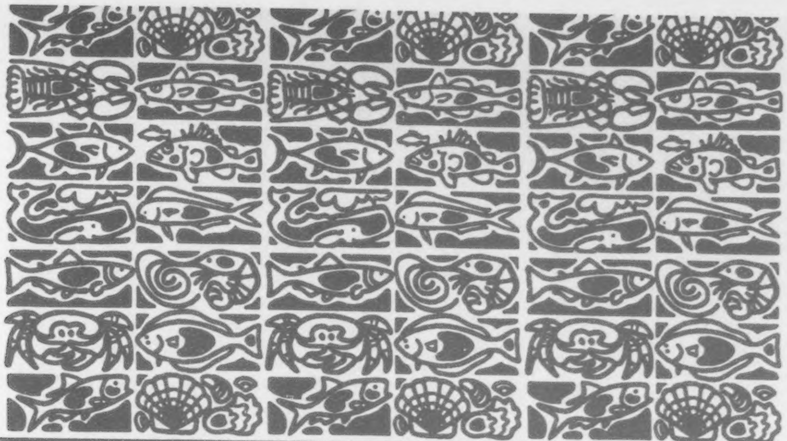

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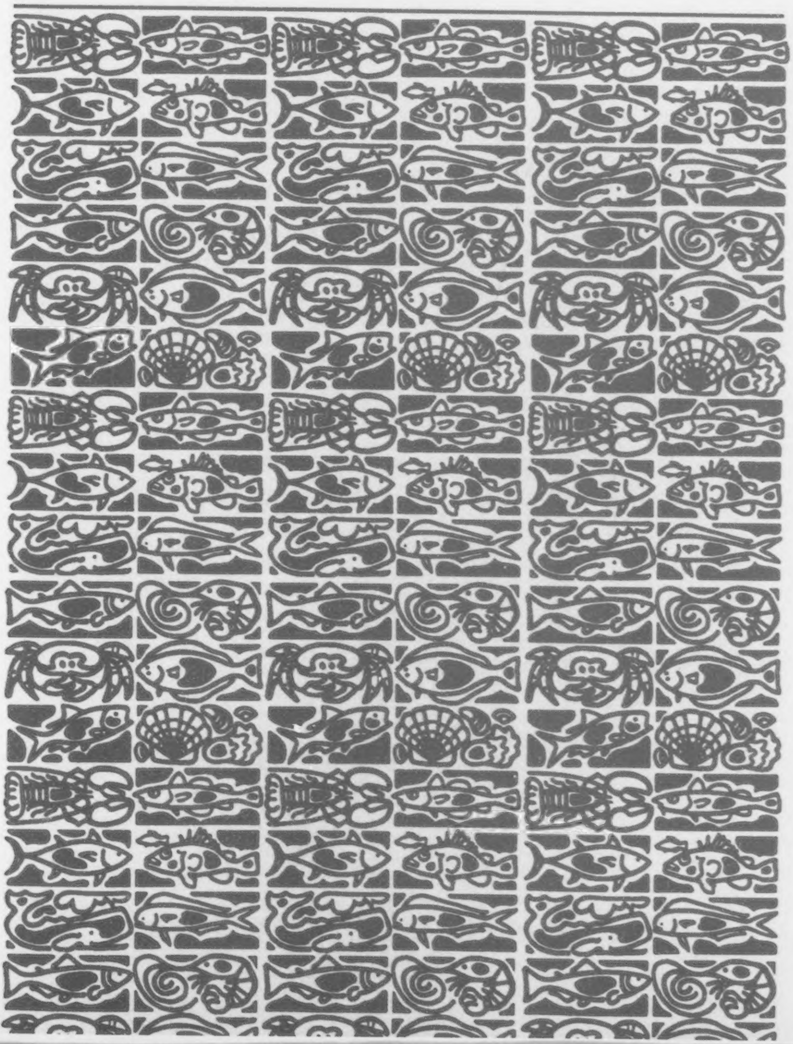

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Abundance of harbor porpoise (*Phocoena phocoena*) in three Alaskan regions, corrected for observer errors due to perception bias and species misidentification, and corrected for animals submerged from view

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Abstract—Estimating the abundance of cetaceans from aerial survey data requires careful attention to survey design and analysis. Once an aerial observer perceives a marine mammal or group of marine mammals, he or she has only a few seconds to identify and enumerate the individuals sighted, as well as to determine the distance to the sighting and record this information. In line-transect survey analyses, it is assumed that the observer has correctly identified and enumerated the group or individual. We describe methods used to test this assumption and how survey data should be adjusted to account for observer errors. Harbor porpoises (*Phocoena phocoena*) were censused during aerial surveys in the summer of 1997 in Southeast Alaska (9844 km survey effort), in the summer oft 1998 in the Gulf of Alaska (10,127 km), and in the summer of 1999 in the Bering Sea (7849 km). Sightings of harbor porpoise during a beluga whale (*Phocoena phocoena*) survey in 1998 (1355 km) provided data on harbor porpoise abundance in Cook Inlet for the Gulf of Alaska stock. Sightings by primary observers at side windows were compared to an independent observer at a belly window to estimate the probability of misidentification, underestimation of group size, and the probability that porpoise on the surface at the trackline were missed (perception bias, $g(0)$). There were 129, 96, and 201 sightings of harbor porpoises in the three stock areas, respectively. Both $g(0)$ and effective strip width (the realized width of the survey track) depended on survey year, and $g(0)$ also depended on the visibility reported by observers. Harbor porpoise abundance in 1997–99 was estimated at 11,146 animals for the Southeast Alaska stock, 31,046 animals for the Gulf of Alaska stock, and 48,515 animals for the Bering Sea stock.

Accurate estimation of abundance of cetaceans from survey data requires careful attention to both survey design and analysis (Buckland et al., 2001). Aerial surveys of cetaceans depend on rapid discovery, recognition, and recording of sightings of individuals and groups of animals by observers, in addition to accounting for animals that were missed because the observers did not notice them (perception bias) or because the animals were below the surface (availability bias) (Buckland et al., 2001). Although an experienced trained observer is efficient at recognition of a species and recording data, it is necessary to include methods that can measure error rates of observers and account for them in the estimation of abundance. We present here the results of a series of aerial surveys designed to estimate the abundance of harbor porpoise (*Phocoena phocoena*) in Alaskan waters.

When, during an aerial line-transect survey, an object or group of objects is encountered, an aerial observer has only a few seconds to complete several tasks: 1) perceive the objects, 2) identify the objects, 3) enumerate the objects, and 4) determine the distance of the objects from the trackline. Items 1 and 4 are the major concern for the estimation of perception bias and for line-transect survey analysis, and it is generally assumed that the observer completes items 2 and 3 correctly or indicates uncertainty correctly (e.g., species code "unidentified porpoise" indicates uncertainty between Dall's porpoise [*Phocoenoides dalli*] and harbor porpoise). We develop methods to test the assumptions of correct species identification and enumeration and apply them to the analysis of line-transect survey data and the estimation of abundance.

From 1991 to 1993, the National Oceanic and Atmospheric Administration (NOAA) conducted aerial surveys in three regions of the Alaskan coast: 1) Cook Inlet and Bristol Bay in 1991; 2) in the waters around Kodiak Island and south of the Alaska Peninsula in 1992; and 3) in the offshore waters of Southeast Alaska from Dixon Entrance to Prince William Sound in 1993. The inside waters of Southeast Alaska were surveyed in each of these years by NOAA crews aboard the NOAA RV *John N. Cobb*. The abundance estimates for these regions were combined to produce an abundance estimate for the Alaska stock of harbor porpoise (Dahlheim et al., 2000). Since then, the Alaska stock has been split into three stocks: Southeast Alaska (SEA), Gulf of Alaska (GOA), and the Bering Sea (BS) stocks (Fig. 1). The 1991–93 abundance estimate was subdivided to correspond with the new stock boundaries (Hill and DeMaster, 1998). To maintain up-to-date stock assessments, abundance

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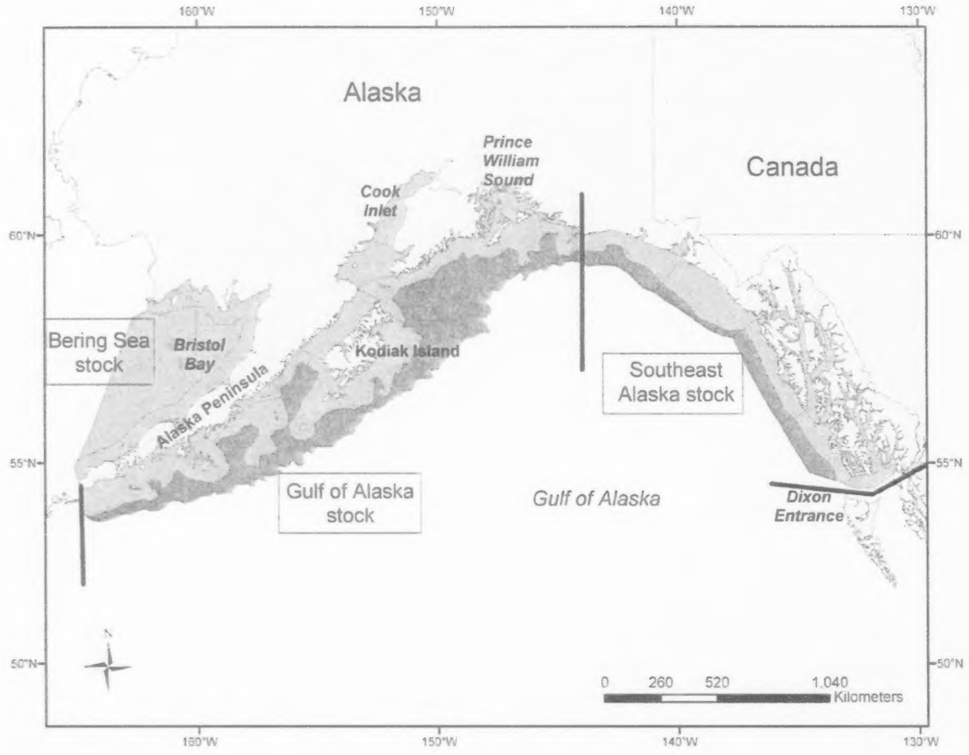

Figure 1

The three harbor porpoise (*Phocoena phocoena*) stock regions in Alaska (Southeast Alaska, Gulf of Alaska, and Bering Sea). The gray shaded areas represent the areas surveyed in 1997– 99, subdivided into areas based on geographical features and depth zones. Dark gray offshore areas were surveyed at one third the effort level per square km than lighter gray nearshore areas. Black lines represent boundaries between stocks.

estimates are required to be based on data not more than 8 years old (Wade and Angliss, 1997). To meet this requirement, abundance surveys of the harbor porpoise stocks in Alaskan waters were conducted from 1997 through 1999.

An important consideration when conducting multiyear surveys is that animals may move from one survey area to another among years and therefore may be counted more than once. Little is known about the year-to-year changes in the distribution of harbor porpoises in Alaska. For two studies of harbor porpoise (*Phocoena phocoena*) on either side of the Atlantic, in the Danish Belt seas (Teilmann et al.[1]) and in the Gulf of Maine (Read and Westgate, 1997), it was concluded that porpoises follow similar movement patterns from year to year and typical ranges of up to 200 km. This finding indicates that a net movement in response to interannual variation in habitat could occur over a range of 100 km. Although this could result in a bias in the estimation of abundance for each stock, depending on the year of the survey, it is not likely that this is a significant occurrence. Each stock region comprises 800 to 1200 km of shoreline so at most approximately 10% to 15% of the region is potentially subject to a net shift in distribution from or into the adjacent stock. Also, the stock boundaries have been chosen to correspond with areas of low harbor porpoise density and therefore there are few animals available to make a shift. These two arguments suggest that if a net shift does occur, it affects at most a small percentage of the population.

This study had three objectives:

1 to present the results of an aerial survey of three harbor porpoise stocks in Alaskan waters during the summers of 1997, 1998, and 1999;

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[1] Teilmann, J., R. Dietz, F. Larsen, G. Desportes, and B. Geertsen. 2003. Seasonal migrations and population structure of harbour porpoises (*Phocoena phocoena*) in the North Sea and inner Danish waters based on satellite telemetry. Abstract in proceedings of annual meeting of the European Cetacean Society, Tenerife, Spain.

2 to produce a correction factor for perception bias that was specific to harbor porpoise in Alaskan waters and to the surveys presented here and to develop methods to test observer performance, by using data collected during these surveys; and

3 to generate abundance estimates for the three stocks of harbor porpoise in Alaska during 1997–99.

Materials and methods

Survey design

Aerial surveys were conducted during June and July beginning with the SEA stock in 1997, proceeding westward through the GOA stock in 1998, and on to the BS stock in 1999. Each study region was divided into areas; 70 areas in Southeast Alaska, 39 areas in the Gulf of Alaska, and 4 areas in the Bering Sea (primarily in Bristol Bay) based on geographical features for inside waters, such as straits and inlets, and two depth zones for offshore waters (Fig. 1). Southeast Alaska was divided into more areas because of its complicated system of waterways, whereas Bristol Bay has relatively homogenous features and therefore was divided into fewer survey areas. Survey effort was stratified by area in Southeast Alaska based on harbor porpoise encounter rates calculated from sightings made in previous surveys (Dahlheim et al., 1993, 1994[2]). The survey transect design each year varied depending on the body of water. In general, the transects in offshore waters were stratified by depth and distance from shore, after an alternating two short and one long sawtooth transect pattern, so that survey effort in the nearshore strata was about three times that in the offshore strata. The 1991–93 surveys were designed with fixed distances of 28 km offshore for the short and 74 km offshore for the long sawtooth tracklines. Our surveys were designed to include the area surveyed in 1991–1993 but also to cover the continental shelf if it extended beyond the original survey. Each set of sawtooths had two criteria and the further offshore of the criteria determined the length of the line. Specifically, in 1997, the short transects in the sawtooth transect pattern extended to a distance of 31 km offshore or the 183-m (100 fm) depth contour, and the long transects extended 74 km or to the 1829-m (1000 fm) depth contour, whichever was farthest from shore. In the 1998 GOA survey, the shelf fell much more gradually in places and funding limited the total survey time. Therefore, the nearshore strata transects were reduced to a distance of 28 km or to the 91-m (50 fm) depth contour, whichever was farthest from shore, whereas the long transects followed the same criteria as in 1997. Because the entire Bering Sea survey region is shallower than 183 m (100 fm), it was covered equally with short transects out to 30 km along the shore and with parallel north–south lines through the center approximately 18 km apart. Smaller bays and inlets were treated separately and stratified by the width of the mouth of the bay or inlet. A subset was chosen to approximate the survey effort by area for the other survey regions, and selection was made on the basis of convenience (i.e., bays and inlets close to the end of survey effort lines were chosen).

Line-transect surveys were flown at an altitude of 152.5 m and a speed of 185 km/h in a DeHavilland Twin Otter aircraft. Survey areas were chosen each day to complete coverage of contiguous areas during weather with winds below 15 knots and at a ceiling above 1000 ft (305 m). Survey lines were broken off and other tracklines with better conditions were sought if the Beaufort sea state exceeded 3 or if visibility dropped to poor for a significant period (at the discretion of the team leader). A primary observer (also referred to as a "side observer") was stationed at the left and right bubble windows of the plane; these positions allowed them to see water directly below the plane. To collect additional sightings and data to estimate perception bias for this study, an independent observer was stationed at a belly window located in the floor at the back of the plane (this observer is also referred to as the "belly observer"). This window provided a circular field of view 100 m (30°) to either side of the trackline and 200 m along the trackline. Five observers rotated in 40-minute shifts through five positions: the right and left bubble windows (primary observers), the belly window (independent observer), a computer station, and a rest position. A headset system was used by the primary observers and computer operator to communicate openly, and the independent observer was isolated and used a string attached to the arm or ankle of the computer operator to indicate a sighting and a notepad to relay information. A simple short hand was developed so that the belly observers would not need to take their eyes off of the trackline.

Survey data were recorded directly to a laptop computer in the airplane using a Turbo PASCAL (vers. 5.0, Borland Software Corp., Austin, TX) language-based software customized for the survey. The software included a proprietary routine (Survey, vers. 3.2, Cascadia Research, Olympia, WA) which read the text output of a global positioning system (GPS) unit connected directly to the serial port of the computer. The date, time, and position of the aircraft were automatically entered into the survey data every minute or whenever other data were entered by the recorder. At the start of each transect, waypoint numbers, observer positions, and environmental conditions were recorded. Environmental conditions included percent cloud cover, Beaufort sea state, visibility (a subjective rating of sighting conditions by each observer at the following levels (excellent, good, fair, poor, and unacceptable), and glare (none, minor, bad, or reflective) experienced by each observer. Visibility was defined as the observer's subjective assessment of the conditions for the likelihood of seeing a harbor porpoise and the observer's assessment of the effect of glare, sea state, as well as less quantifiable factors such as turbidity, sun angle, unusual weather conditions, and fatigue on the observer's ability to sight a harbor porpoise. The observers reported these environmental data as changes in such data were noticed along a transect. For each sighting, the observer notified the computer operator when the beam line of the plane crossed the animal's location. The primary observers used inclinometers to obtain the vertical angle below the horizontal to convert the perpendicular distance of the animal from the trackline (Lerczak and Hobbs, 1998). To determine the distance of a sighting from the trackline indicated by a center line on the belly window, the window was subdivided with a grease pencil into six 10°-bins (out to 30° to either side of the trackline for an averaged eye height), labeled 1–6 from port to starboard. When alerted to a sighting by the primary or independent observers, the computer operator immediately entered the sighting by using a hot key assigned to an observer (which recorded the observer's initials and which captured the time and position from the GPS unit). The hot key also opened a window for entering species name, vertical angle or angle bin, group size, and any notable animal behavior.

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[2] Dahlheim, M., A. York, J. Waite, and R. Towell. 1993. Abundance and distribution of harbor porpoise (*Phocoena phocoena*) in Southeast Alaska and Western Gulf of Alaska, 1992. 1992 Annual report to the Marine Mammal Protection Act (MMPA) Assessment Program, 52 p. Office of Protected Resources. NMFS, NOAA, 1335 East-West Highway, Silver Spring, MD.

Matching sightings from side and belly windows

Sighting data (time, perpendicular distance, species, and group size) collected on the same transects were compared between side and belly observers. For comparison purposes, left- and right-side sighting angles were converted to corresponding belly observer bin number. Sightings were considered matches (same group seen by both observers) if they 1) occurred within 5 seconds of each other; 2) were not greater than one 10° bin difference; and 3) met other conditions such as a species of similar size or of hierarchical relation (e.g., harbor porpoise matched to unidentified small cetacean) and similar group size. Matched sightings were used 1) to estimate an empirical average angle for each belly window bin, based on the angles measured from the side windows; 2) to identify circumstances resulting in unreliable species identifications (see *Errors in species identification* in Appendix I); 3) to estimate bias in group-size estimates by the belly observer; 4) to estimate perception bias and $g(0)$ (here $g(0)$ accounts only for the consequences of perception bias; correction for availability bias is treated separately as described below); and 5) to eliminate duplicate sightings from the distance analysis.

Correction for bias in group-size estimates determined by belly observers

Initial inspection of the data when both the side and belly observers reported a sighting indicated that the group size estimate of the belly observer was occasionally less than that provided by the side observer—a result of the restricted visual field and limited observation time for the belly observer. For each of these pairs, the count by the side observer was divided by the count by the belly observers. These ratios were then grouped by belly observer group size and averaged to estimate a correction for each group size reported by the belly observer. The standard error for each correction factor was estimated by the usual formula. The correction was applied to all group sizes from belly sightings included in the average estimate of group size.

Distance smearing

Angle rounding occurred in both the side observer data and the belly observer data. In the case of the side observer data, peaks in frequency occurred on multiples of 5°. The rounding of angles often occurred after the sighting was out of the field of view and the observer estimated the angle from a remembered location. The accuracy for these remembered locations may not have been any better than 5°, and therefore created a tendency for observers to use a close 5° increment number rather than one of the marks in between. Belly observer data were assigned to a bin and were thus automatically rounded. To remove these effects, side sightings were dithered uniformly over 13 m (2.5° on either side of the reported angle) and belly sightings were dithered uniformly over 26 m (5° on either side of the reported angle, the center of sighting bins). The dithering distance was chosen empirically as the minimum distance necessary to remove the rounding effect. The dithering was repeated several times and the cumulative distribution of the sightings by distance to the trackline was examined. An instance of the dithering which gave a visually smooth distribution was retained and used as the data set for further analysis to estimate the sighting distribution.

Estimation of perception bias and $g(0)$

All three years of data were combined to estimate perception bias from comparisons of the primary and the independent observer sightings. Logistic regression with a generalized linear model (the GLM function in S-PLUS, Lucent Technologies, Murray Hill, NJ) and an offset algorithm for comparison of paired sightings (Buckland et al., 1993) was used to estimate the perception bias of the side and belly observers on the trackline. Review of the ratio of matched to unmatched sighting for the belly and side observers by 25-m bins indicated that the two inner bins were consistent with each other (0–25 m and 25–50 m), whereas the outer bin (50–75 m) differed. Consequently, perception bias was estimated by using only sightings within 50 m of the trackline (approximately 20° at the standard survey altitude or bins 2 through 5 in the belly window). Sightings beyond this cutoff distance were excluded. Possible covariates in the logistic regression were visibility, sea state, cloud cover, glare, group size, observer, and survey year. Covariates were initially tested individually to identify functional forms or groupings that could reduce the number of parameters necessary to represent them. The discrete covariates (visibility, sea state, glare, group size, observer, and survey year) and the continuous covariate cloud cover (grouped into five categories: 0–20%, 20–40%, 40–60%, 60–80%, 80–100%), were examined individually as categorical factors. The coefficients from the categorical analysis were then charted against their hierarchical ranks. Where the coefficients appeared to fit a simple functional form of the hierarchical ranks (line, square root, natural logarithm, exponential) or could be grouped to reduce the number of parameters, the analysis was repeated with this alternative. The parameters for the function or grouping were estimated by using the regression described above and compared to the result of the categorical factor by using Akaike's information criterion (AIC). The function or grouping was used in the subsequent analysis if it improved the AIC. From this preliminary analysis, visibility and sea state were found to have a nearly linear effect and were treated as linear functions by using the hierarchical number as the value and by setting the best condition to one; group size was also considered to be linear. Cloud cover, glare, observer, and survey year were considered as categorical data. Significant covariates were then combined in the GLM model and removed in a stepwise manner until the AIC had been minimized. The perception bias for each observer position and each transect segment was estimated from the final model and combined to estimate $g(0)$ for each transect segment (see Appendix II for details).

The program DISTANCE, vers. 3.5 (Thomas et al., 1998) allowed only a global $g(0)$ and thus did not accommodate $g(0)$ to be estimated for each transect segment from environmental and observer covariates. It was possible to circumvent this limitation by adjusting the length of each trackline to allow an estimate of density in the vicinity of each trackline because $g(0)$ and length are multiplied together to estimate density. The estimates of $g(0)$ for each transect segment were averaged for all three years weighted by the transect lengths to estimate an average $g(0)$. The length of each transect segment was multiplied by its estimated $g(0)$ divided by the average $g(0)$ to generate an adjusted transect segment length which accounted for the $g(0)$. The adjusted transect segment lengths were then used in DISTANCE in place of the actual lengths and the average $g(0)$ calculated above was used as the global $g(0)$ in DISTANCE. The standard error for the global $g(0)$ was estimated as the weighted average of the standard errors of the $g(0)$ estimates for the individual transect segments.

Estimation of abundance

The line-transect analysis program DISTANCE (vers. 3.5) was used to estimate the observed density of harbor porpoise in each surveyed region. Two sighting probability curves were estimated so that for transect segments with usable belly observer effort data, sightings from the side and belly observers could be combined and duplicates removed or, when no belly observer data were available, sightings from the side observers only could be used. To identify significant effects of possible covariates for estimated strip width (presence or absence of a belly observer, survey year, individual observers, visibility levels, glare types, percent cloud cover, and sea state), each factor was considered separately as a covariate and the one with the lowest value for the AIC was retained. This process was repeated with the remaining possible covariates in an additive manner until further addition of covariates did not lower the AIC. Distances were pooled into 50-m bins to allow application of the estimate of perception bias. Densities were estimated for the individual areas with usable survey data. Unsurveyed areas such as the small bays and inlets were assigned the average densities from the surveyed areas of that stratum. These densities were then averaged, weighted by the area of each survey region, to estimate an average observed density and abundance for each stock. Variances were calculated as in Buckland et al. (2001). The correction factor for availability bias is the inverse of the estimate of availability from Laake et al. (1997) ($2.96=(1/0.338)$, $CV=0.18$). This factor was applied as a multiplier to the observed abundance estimates to produce the abundance estimate for each stock.

Incorporation of other survey data

The vast area comprising Alaska waters made it impossible to survey all areas where harbor porpoises occur. Harbor porpoise sighting data were available from a concurrent NMFS beluga whale line-transect survey in Cook Inlet. For this survey, an Aero Commander aircraft with bubble windows was used; however, the windows were smaller than those of the Twin Otter aircraft, and the observers could not see directly below the plane. Survey methods were similar, except that the beluga whale survey was conducted at an altitude of 244 m and the primary focus was beluga whales. The search effort, therefore, was not concentrated as close to the trackline as it would have been if the survey had been designed to survey harbor porpoise. NMFS National Marine Mammal Laboratory has conducted these beluga whale surveys each year since 1993. We estimated abundance for harbor porpoise in Cook Inlet using the 1998 survey data, a strip width estimated from all beluga surveys (1993 to 1999), and the correction for availability bias from Laake et al. (1997). Perception bias could not be estimated for this survey. This abundance estimate was added to the abundance estimate from the GOA survey to produce a combined estimate for that stock.

Minimum abundance estimate

A minimum abundance estimate, $N_{\min}$, defined in Wade and Angliss (1997) as the lower 20th percentile of the lognormal error distribution, is used in management

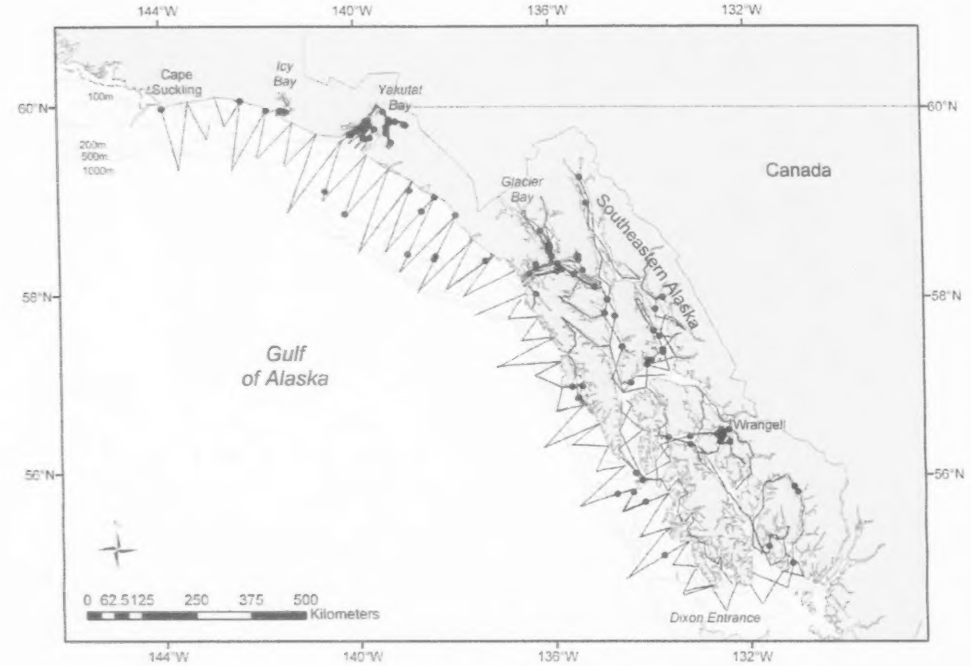

Figure 2

Completed survey transects and sightings (circles) of harbor porpoise (*Phocoena phocoena*) during the 1997 aerial survey in the Southeast Alaska stock region.

decisions by NMFS. This quantity was calculated for each stock from the completed abundance estimates as

$$N_{\min} = Ne^{-0.842\left[\sqrt{\ln(1+CV(N)^2)}\right]},$$

where N = estimated abundance; and
$CV(N)$ = the estimated coefficient of variation of N.

Results

The 1997 line-transect aerial survey was conducted from 27 May to 7 June and 10–28 July 1997 in the inside waters of southeastern Alaska, Yakutat Bay, Icy Bay, and in offshore waters from Dixon Entrance to Cape Suckling (Fig. 2). Necessary repairs on the survey plane resulted in an unplanned month-long break in the survey, and adverse weather prevented a second survey of offshore waters. A total of 9844 km were surveyed. The 1998 survey was conducted from 27 May to 28 July 1998 in Prince William Sound, the western Gulf of Alaska (from Cape Suckling to the west side of Kodiak Island), and Shelikof Strait (Fig. 3). Gaps in the survey effort occurred on account of inclement weather, primarily off the Kenai Peninsula and the southern side of the Alaska Peninsula west of Kodiak Island. A total of 9486 km were surveyed. The 1999 survey was conducted 11 June to 4 July in Bristol Bay and associated bays. In addition, an area south of the Alaska Peninsula west of Chignik Bay was surveyed that was not completed in 1998 (Figs. 3 and 4). A total of 8490 km were surveyed. The 1999 data for the Gulf of Alaska was included with the 1998 data to estimate abundance of harbor porpoise for the Gulf of Alaska.

Sightings of harbor porpoise for each region (Figs. 2–4) were more common in nearshore areas, but occurred throughout the depth range surveyed during all three surveys. High densities of harbor porpoise were found in Yakutat Bay and near Wrangell (Fig. 2), between Prince William Sound and Cape Suckling, on the southeast side of Kodiak Island, southwest of Chignik Bay (Fig. 3), and in a few small bays on the northern side of Bristol Bay (Fig. 4).

Corrections for species misidentification and for under-counting group sizes by belly observers

A cursory examination of the discrepancies in species identification between side and belly observers from the 1997 and 1998 seasons indicated that discrepancies occurred primarily when inexperienced observers were at the belly window and had fewer than 10 days of

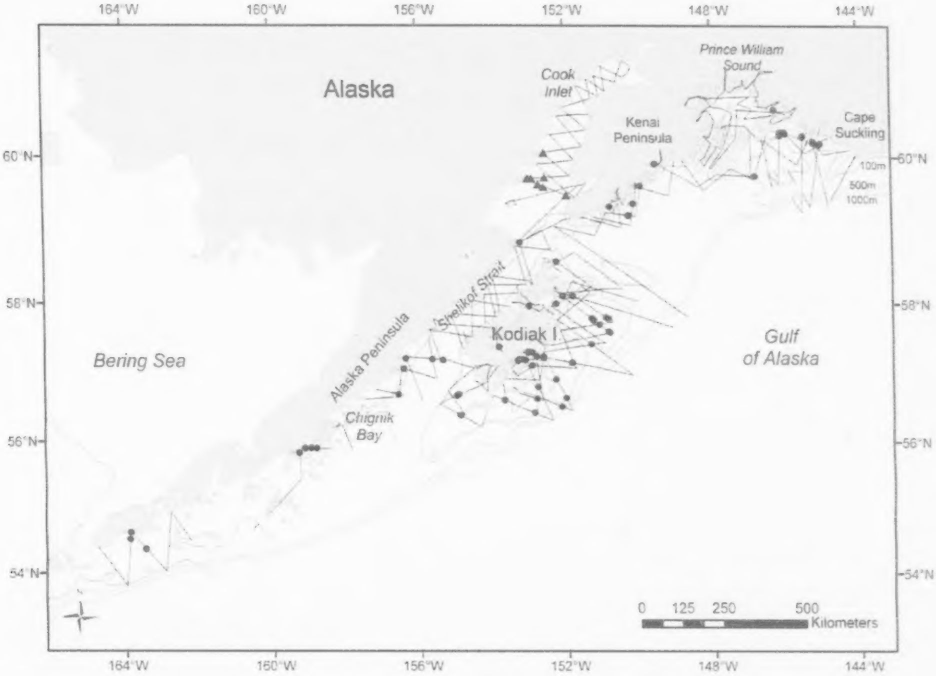

Figure 3

Completed survey transects and sightings (circles) of harbor porpoise (*Phocoena phocoena*) during the 1998 aerial survey and the 1998 beluga whale aerial survey (triangles) in the Gulf of Alaska stock region. Also shown are transects and sightings of harbor porpoise made during the 1999 aerial survey south of the Alaska Peninsula and west of Chignik Bay.

survey experience. Based on this *ad hoc* assessment of discrepancies, an experienced observer was defined as one who had 10 or more days of observation experience on the survey. Species discrepancies involving harbor porpoise were those that led to a misidentification of harbor porpoise as either a Dall's porpoise or harbor seal (*Phoca vitulina*).

Within the data from the first two years of the survey, there were 68 species identifications of harbor porpoise, Dall's porpoise, and harbor seal from paired observers. Of these 68 identifications, 52 were determined by paired experienced observers in the side and belly (one discrepancy), 12 were determined by an experienced side observer paired with an inexperienced belly observer (4 discrepancies), and 4 were determined by an inexperienced side observer paired with an experienced belly observer (no discrepancies). No correlation between discrepancies and environmental conditions was found. To verify the observation that the inexperienced observers in the belly position had a higher than average misidentification rate and determine if the rate was unacceptable, four possible models were compared and AIC was used to identify the most parsimonious model. The models were 1) side observers and experienced and inexperienced belly observers were all different (four parameters); 2) experienced and inexperienced side observers and experienced belly observers were equivalent and inexperienced belly observers were different (two parameters); 3) experienced and inexperienced observers were different but side and belly were equivalent (two parameters); and 4) all observers were equivalent (one parameter). For model 1, probabilities of a correct identification were >0.99 for both experienced and inexperienced side observers, 0.98 for experienced belly observers, and 0.67 for inexperienced belly observers with an AIC of 13.0. For model 2, side observers with experienced belly observers had a probability of 0.98, and inexperienced belly observers had a probability of 0.67 with an AIC of 9.1. Model 3 resulted in a probability of 0.99 for experienced observers and >0.76 for inexperienced observers with an AIC of 11.6. Model 4, a probability for all observers, was 0.96 with an AIC of 17.6. The most parsimonious model (lowest AIC) was model 2, indicating that an inexperienced observer in the belly position had a low reliability for species identification. Consequently, observation effort and sightings by inexperienced observers in the belly during their first 10 survey days were treated as practice and were not included in the subsequent analysis. Although it would be possible to estimate a $g(0)$ that accounted

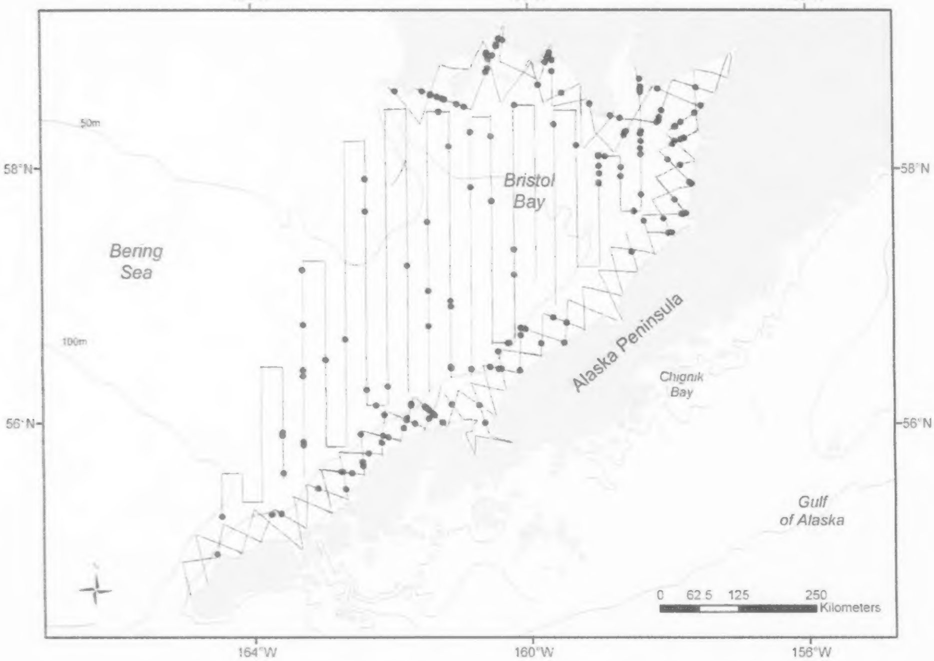

Figure 4

Completed survey transects and sightings (circles) of harbor porpoise (*Phocoena phocoena*) during the 1999 aerial survey in the Bering Sea stock region. Transect and sightings on the south side of the Alaska Peninsula are shown in Figure 3 as part of the Gulf of Alaska survey.

for the inexperienced observers in the belly, we did not have the estimate of the density for the other species necessary to complete this calculation.

Group size was typically underestimated by the belly observer in comparison to the side observers. In sightings by both the belly and side observers, separate corrections were calculated for group sizes reported as one individual and groups reported as two individuals by the belly observer. Of 30 groups reported as one harbor porpoise by the belly observer, 25 were reported as a group size of one by the side observer and 5 were reported as a group size of 2, yielding a multiplicative correction of 1.167 (CV=0.059) groups of size one seen only by the belly observer. Likewise, of 12 groups reported as two harbor porpoise by the belly observer, 11 were reported as a group size of 2 by the side observer and one was reported as a group size of 3, yielding a multiplicative correction of 1.042 (CV=0.080) for groups of 2 observed from the belly of the aircraft . The group-size estimate from the side observer was used when a group was reported by both the side and belly observers. The correction was only applied to group size when the group was seen only by the belly observer. A correction for total animals was estimated as the sum of the group sizes with the belly-window–derived groups sizes corrected, divided by the sum of the group sizes with the belly-window–derived group sizes uncorrected. As a result, a multiplier of 1.018 (CV=0.006) was applied to the abundance estimates. It was necessary to apply a general correction rather than correct individual group sizes to avoid problems with the $g(0)$ estimate and DISTANCE analysis arising from non-integer group sizes.

Estimation of perception bias and $g(0)$

Comparisons between sightings by the belly observer and the side observers indicated that each missed a small but significant fraction of the near-surface animals on the trackline. A total of 129 potential matches between experienced belly observers and independent side observers within 50 m of the trackline were examined for perception bias and $g(0)$ estimation. Although several of the potential covariates were significant by themselves, only visibility as a continuous variable remained in the stepwise elimination. A significant difference in estimated strip width between survey year 1997 and the years 1998 and 1999 was identified in the distance analysis and, therefore, year was included as a covariate as well. Although year was not a significant coefficient, there was a significant turnover in personnel from the

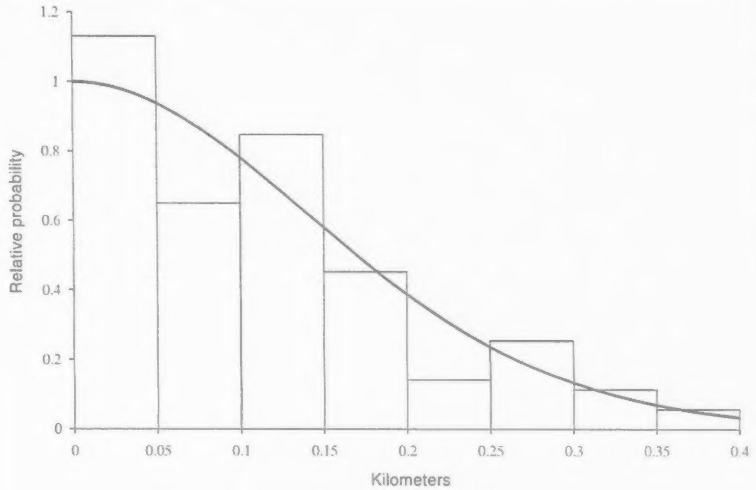

Figure 5

Relative probability of detection of harbor porpoise (*Phocoena phocoena*) by distance from the survey trackline (km) determined with a half-normal model for the 1997 sighting data of harbor porpoise in the Southeast Alaska stock region. The histogram shows the distribution of sightings in 0.05-km groups.

first to the second and third years, and 1997 was the first year of a belly observer for the survey leaders. The belly observer had a significantly higher probability of sighting an available group than the side observers for any particular sighting, and the belly observers routinely reported better visibility than did the side observers. This difference in perception bias was accounted for by the difference in reported visibility. The logistic regression coefficients were as follows: constant=1.187 ±0.542, (t=2.19); for year=0 for 1997 and 1 for 1998, 1999, coefficient=0.296 ±0.290, (t=1.02); for visibility=1 (excellent), 2 (good), 3 (fair), 4 (poor), 5 (unacceptable) as a continuous variable, coefficient=−0.502 ±0.217, (t=−2.31). The model for probability of sighting of an available group for a single observer is then

$$P\left(sighting \middle| year, visibility\right) = \frac{e^{1.187+0.296\,year-0.502\,visibility}}{1+e^{1.187+0.296\,year-0.502\,visibility}}.$$

Heterogeneity in probability of sighting a harbor porpoise resulted in a decrease of a difference of roughly 0.11 for each reduction in visibility and an increase by roughly 0.06 from 1997 to 1998–99 (Table 1). The average observed $g(0)$ values (perception bias only) for the SEA stock, the GOA stock, and BS stock of harbor porpoise were 0.641 ±0.069, 0.729 ±0.048, and 0.748 ±0.046, respectively, and yielded average perception bias correction factors of 1.560 (CV=0.108), 1.372 (CV=0.066), and 1.337 (CV=0.062), respectively (Table 2).

Estimated strip width for observations

Variation in effective strip width (ESW) occurred for the configuration of observers and visibility as reported by the observers. Few sightings occurred beyond 400 m and therefore this distance was chosen as the truncation point for distance from the trackline and sightings beyond this distance were not included in the analysis. Effort was separated into effort with and without a belly observer. ESW without a belly observer was the ESW on one side of the plane covered by a side observer. ESW with a belly observer represented the effort of one side observer and half of the belly observer because the belly observer's field of view was divided by the trackline (note that duplicate sightings were removed such that where sightings were reported by both the side and belly observer, only the side sighting record was used). The ESW for 1997 was significantly different from that of 1998 and 1999; therefore they were treated separately (Table 1). In the 1997 data, significant variation in ESW was related to visibility level and in the 1998 and 1999 data, to the presence or absence of the belly observer. The best fit for the detection function was a half-normal curve for the 1997 data set and a half-normal curve with a one term cosine correction for the 1998–99 data set (Figs. 5 and 6, Table 2). The ESW of the survey team in 1997 decreased by roughly 20% per step change in visibility. When this decrease in ESW was combined with approximately a 12% decrease in $g(0)$ with each step in visibility, the product (Table 1) indicated an

Table 1

Estimated $g(0)$ (probability of detecting an animal at the surface on the trackline (perception bias) and effective strip width (ESW) in km for harbor porpoise in Alaska determined from surveys from 1997 through 1999. Data were obtained from individual observers and teams of observers, all of whom reported the same visibility code. The product of these two values, $g(0)$ and ESW, is a measure of the relative effectiveness of the observer team under different conditions. Single observer=single observer at either the right, left, or belly window of aircraft. Team of observers=a team of observers at the right, left, and belly window of the aircraft.

		Single observer				Team of observers			
		1997		1998–99		1997		1998–99	
Visibility		Value	SE	Value	SE	Value	SE	Value	SE
1 (excellent)	$g(0)$	0.66	0.08	0.73	0.06	0.89	0.01	0.93	0.01
	ESW	0.252	0.022	0.139	0.008	0.252	0.022	0.118	0.007
	$g(0)$ESW	0.166	0.009	0.101	0.004	0.224	0.002	0.11	0.001
2 (good)	$g(0)$	0.55	0.06	0.62	0.04	0.79	0.02	0.85	0.01
	ESW	0.2	0.017	0.139	0.008	0.2	0.017	0.118	0.007
	$g(0)$ESW	0.11	0.004	0.086	0.002	0.158	0.003	0.1	0.001
3 (fair)	$g(0)$	0.42	0.07	0.49	0.06	0.66	0.04	0.74	0.02
	ESW	0.153	0.013	0.139	0.008	0.153	0.013	0.118	0.007
	$g(0)$ESW	0.064	0.002	0.068	0.002	0.101	0.003	0.087	0.001
4 (poor)	$g(0)$	0.31	0.1	0.37	0.09	0.52	0.11	0.61	0.08
	ESW	0.116	0.01	0.139	0.008	0.116	0.01	0.118	0.007
	$g(0)$ESW	0.036	0.001	0.051	0.002	0.06	0.003	0.072	0.004
5 (unacceptable)	$g(0)$	0.21	0.11	0.26	0.12	0.38	0.19	0.46	0.16

approximately 30% decrease in effective effort with each step in visibility and that survey effort during poor conditions had less than one quarter of the effectiveness of effort during the best conditions (Fig. 7). In the 1998–99 surveys (Fig. 8), the ESW was narrower overall and slightly broader when the belly observer was not present. Although this seems counterintuitive, it is the result of a peak that occurred near the trackline when the belly sightings were included and which made the distribution away from the trackline relatively lower and resulted in the narrower ESW (Table 1, Fig. 8). When ESW and $g(0)$ were multiplied together, the added value of the belly observer was 10% under the best conditions and nearly 50% under poor conditions.

Density and abundance of harbor porpoise

Abundance estimates of harbor porpoise increased from east to west as did estimates of average density by stock (0.10, 0.19, and 0.44 porpoise/km^2, respectively). Average observed harbor porpoise densities (uncorrected for availability or perception biases) for the SEA, the GOA, and the BS stocks were 0.033 groups/km^2 (CV=17.2%), 0.062 (CV=11.9%), and 0.153 (CV=13.2%), respectively. Approximately 5% of the study areas, consisting primarily of inlets and channels, were unsurveyed. Density estimates for these unsurveyed areas were extrapolated from similar surveyed areas in the same general region (Table 3). The correction factor of 2.96 (CV=0.180) (Laake et al., 1997) was applied to each abundance estimate to account for availability bias. The full corrections for visibility bias (correction for perception bias × correction for availability bias) were 4.62 (SEA, CV=21%), 4.06 (GOA, CV=19%), and 3.96 (BS, CV=19%).

For the Cook Inlet survey, the effective strip width (0.280 km, CV=0.281) was based on 44 sightings from the 1993 to1999 surveys. Truncation of the sighting strip by discarding sightings less than 0.1 km from the trackline or greater than 0.6 km from the trackline on each side of the plane was necessary to obtain a good fit of the detection function. The best fit for the detection function for the Cook Inlet data, based on AIC, was a hazard-rate curve with a cosine correction (Fig. 9). The 1998 beluga whale survey in Cook Inlet resulted in eight harbor porpoise sightings along 1355 km of trackline. No data were available to estimate the perception bias for this survey and its format was sufficiently different from the harbor porpoise survey with the result that it was uncertain whether the perception bias correction would be approximately correct. Consequently, only the correction for availability (2.96, CV=0.180) was applied. This results in a rather conservative estimate with a known negative bias which we feel is preferable to one with an unknown bias.

The abundance estimate for the SEA stock of harbor porpoise was 11,146 animals (CV=24.2%; $N_{\min}$=9116,

Table 2

Survey parameters and abundance estimates for harbor porpoise (*Phocoena phocoena*) stocks off Southeast Alaska, the Gulf of Alaska, and the Bering Sea in 1997, 1998, and 1999, respectively. Cook Inlet survey results are taken from a survey for beluga whales which followed a protocol similar to the harbor porpoise surveys. No perception bias correction was available for the 1998 Cook Inlet survey; consequently observed abundance is used in place of total abundance for this area. The Cook Inlet abundance was included in the Gulf of Alaska stock total abundance. Extrapolated areas were small inlets and unsurveyed areas where the density of harbor porpoise was assumed to be the same as similar surveyed areas for the purpose of estimating total abundance. Coefficient of variation (CV) of a statistic is the standard error of the statistic divided by the statistic; confidence intervals are calculated by using a log-normal distribution and $N_{min} = Ne^{-0.842\sqrt{\ln(1+CV(N)^2)}}$.

	Southeast Alaska		Gulf of Alaska		Cook Inlet Survey		Bering Sea	
	Estimate	CV(%)	Estimate	CV(%)	Estimate	CV(%)	Estimate	CV(%)
Study region (km^2)	106,087		158,733		18,948		106,381	
Total trackline (km)	9844		10,127		1355		7849	
No. if sightings	129		88		8		201	
Average correction for perception bias (1/g(0))	1.560	10.8%	1.372	6.6%	1		1.337	6.2%
Effective half strip width (km)	0.182	8.7%	0.122	5.8%	0.280	28.1%	0.122	5.8%
Average group size (no. of individuals)	1.279	4.4%	1.289	2.3%	1.129	5.0%	1.289	2.3%
Corrected average group density (groups/km^2)	0.026	16.6%	0.048	11.7%	0.012	60.5%	0.119	13.0%
Average porpoise density (porpoise/km^2)	0.033	17.2%	0.062	11.9%	0.013	60.7%	0.153	13.2%
Uncorrected abundance in surveyed areas	3505	17.2%	9791	11.9%	249	60.7%	16,289	13.2%
Extrapolated area (km^2)	6539		4722					
Abundance in extrapolated area	261	40.5%	449	60.6%				
Total uncorrected abundance	3766	16.2%	10,489	11.5%			16,289	13.2%
Correction for availability (from Laake, et al., 1997)	2.96	18.0%	2.96	18.0%			2.96	18.0%
Average perception correction × availability correction	4.62	21.0%	4.06	19.2%	2.96	18.0%	3.96	19.0%
Total abundance (N)	11,146	24.2%	31,046	21.4%			48,215	22.3%
N_{min}	9116		25,987				40,039	
Lower 95% confidence limit	6980		20,520				31,285	
Upper 95% confidence limit	17,788		46,972				74,308	

Table 1). The abundance estimate for the GOA stock, which included the Cook Inlet harbor porpoise abundance estimate, was 31,046 animals (CV=21.4%; N_{min}=25,987, Table 1), and the abundance estimate for the BS stock was estimated as 48,215 animals (CV=22.3%; N_{min}=40,039, Table 1).

Discussion

Habitat type may account for the increase in density of harbor porpoise from east to west—at least for the much higher abundance of the BS stock compared to the other two stocks. The Bering Sea encompasses a vast sea ranging from a large shallow bay (Bristol Bay) extending to a large shelf that descends to the abyssal sea. Our entire survey of this stock region was conducted in Bristol Bay where water depth never exceeds 100 m. In contrast, the shelf area is narrower in the Gulf of Alaska so that the surveys off Southeast Alaska and in the Gulf of Alaska were routinely conducted in waters up to 200 m, and occasionally up to 1800 m. Despite the greater ranges of depths surveyed in Southeast Alaska and the Gulf of Alaska, harbor porpoise were present primarily in waters less than 100 m in depth. Off northern California, higher than expected numbers of harbor porpoise were found between the 20 m to 60 m isobaths and fewer than expected in waters deeper than 60 m (Carretta et al., 2001). Similarly, Barlow (1988) found harbor porpoise primarily distributed in waters shallower than 110 m in depth. In contrast, Raum-Suryan and Harvey (1998) found that harbor porpoise near the northern San Juan Islands, Washington, were present at depths greater than 100 m. Differences in

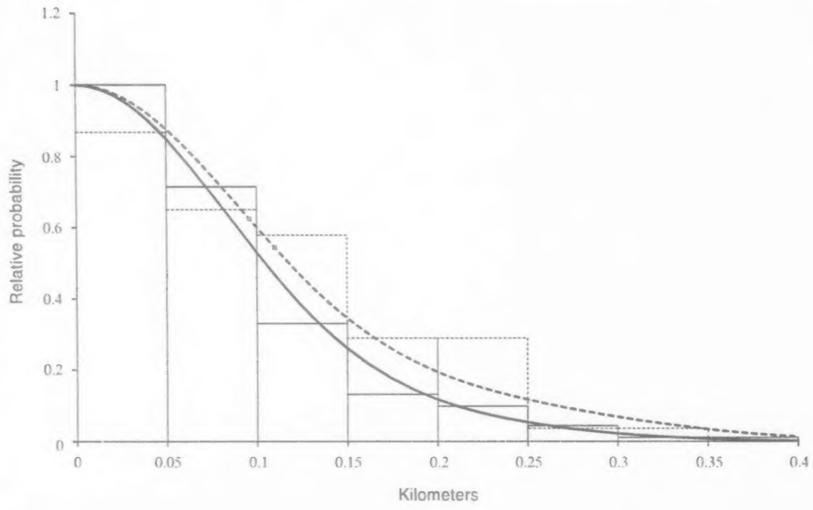

Figure 6

Relative probability of detection of harbor porpoise (*Phocoena phocoena*) by distance from the survey trackline (km) determined with a half-normal model with cosine adjustment for the 1998 and 1999 harbor porpoise sighting data. The solid line represents the probability of a sighting when both side observers and a belly observer were present. The dashed line represents the probability of a sighting when only side observers were present (without a belly observer). The histogram shows the distribution of sightings in 0.05-km groups.

harbor porpoise occurrence by depth may account for the higher density estimated for the Bering Sea stock; however, the survey comprised only a portion of the entire stock.

The SEA stock abundance estimate is not significantly different from the 1991–93 abundance estimate. The abundance estimates for the GOA stock (31,046) and the BS stock (48,215) are significantly higher than the 1991–93 abundance estimates (8497 and 10,946, respectively) (*t*-test, natural log of means, $P<0.01$). It should be noted that the GOA stock abundance estimate may be biased low because it includes a survey of Cook Inlet which could not be corrected for perception bias, and the BS stock may have been underestimated as described in the previous paragraph. However, differences in survey design with the earlier surveys confound direct comparison between the abundance estimates. Overall, the area covered in the 1997–99 surveys was larger than that of the 1991–93 surveys and included a wider range of possible harbor porpoise habitat. The 1997–99 surveys were designed to include a sample of bays and inlets within the study region that the earlier surveys did not sample. The 1997–99 survey also included some larger bodies of water, such as Icy Bay and the inside waters of Southeast Alaska, that were not included in the earlier survey and gave more thorough coverage to some areas such as Yakutat Bay and Prince William Sound. The offshore extent of the 1997–99 survey was determined by water depth rather than distance, which extended it farther offshore in the Southeast Alaska and Gulf of Alaska stock regions. The 1999 survey in the Bering Sea stock region covered much of the same area as the 1991 survey but at a higher density of effort. In 1999, the survey area to the south of the western end of the Alaska Peninsula (a survey area that was not completed in 1998) was surveyed. This area was not surveyed in the 1991–93 surveys. The survey design allowed for the inclusion of potential harbor porpoise habitat that was not covered in the previous surveys, especially areas such as Yakutat Bay and Sitkalidak Strait (Kodiak Island). Another difference between the surveys was the use of correction factors. A perception-bias correction was estimated from independent observer data, and therefore only the Laake et al., 1997 correction of 2.96 for availability bias was required to make a combined visibility correction factor of 4.62 for the SEA stock, 4.06 for the GOA stock, and 3.96 for the BS stock; these correction factors are 49%, 31%, and 28%, respectively, larger than the factor of 3.1, used in the 1991–93 surveys (Hill and DeMaster, 1998). The correction factors used in our analyses better reflect conditions encountered during aerial surveys for porpoise in Alaska because they incorporate a direct measure of animals missed by observers during the surveys, as well as the best available estimate of the animals missed while out of view underwater.

It is likely that the shorter sighting time for the observer in the belly window increased the probability that inexperienced observers misidentified species of similar size during observations. Observers in the belly position of the aircraft during this survey had approximately 2–4 seconds to perceive, identify, and enumerate a group of animals. This is about half of the time available to the side observers and leaves little time for the observer to double check cues to distinguish among species. Thus, the observers are left with their first impressions which may be mistaken if there is little prior experience in observing and recording individual and groups of harbor porpoises. Laake et al. (1997) found a difference in perception bias between experienced ($g(0)=0.86$) and inexperienced ($g(0)=0.23$) observers in an experiment where the sighted species was known. We concur with Laake et al. (1997) that experienced observers should be positioned at the belly window and a training period should be considered for new aerial observers before their data from the belly position is used to estimate $g(0)$.

This analysis was completed in 2000 with the software that was available (DISTANCE, vers. 3.5), which did not include features to use multiple resights, so that perception bias had to be estimated separately. The current software DISTANCE 5.0 can use multiple resight data to estimate perception bias but does not correct for bias in the estimation of group size or for errors in species identification. Although some of the components of the analysis presented here are now completed automatically within the current software, the analysis of observer performance would have to be completed separately.

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Table 3

Estimates of abundance of harbor porpoise (*Phocoena phocoena*) in unsurveyed inlets and channels for the 1997–99 aerial surveys in Alaska. Density of harbor porpoise was averaged for similar areas that were surveyed and then used to extrapolate density and abundance in the similar unsurveyed areas. These extrapolated abundances were summed by stock and included in the total abundances of the Southeast and Gulf of Alaska stocks.

	Southeast Alaska stock			Gulf of Alaska stock				
	Southeast Alaska	Frederick Sound	Southeast Alaska total	Kenai Peninsula	Kodiak Island	Alaska Peninsula	Prince William Sound	Gulf of Alaska total
Number of comparable areas (e.g., inlets and channels) surveyed	32	2	34	3	9	2	5	19
Area surveyed (km^2)	4792	2564	7356	439	2782	202	4188	7611
Weighted average porpoise density in surveyed regions	0.037	0.080		0.130	0.151	0.092	0.008	
Weighted standard deviation of densities	0.129	0.058		0.071	0.255	0.423	0.020	
Number of unsurveyed areas	326	1	327	15	17	21	9	62
Unsurveyed area (km^2)	6135	404	6539	662	1356	1617	1087	4722
Estimated abundance in unsurveyed areas	229	32	261	86	205	149	8	449
Standard error of abundance for unsurveyed regions	103	24	106	20	143	230	11	272
% Coefficient of variation of abundance for unsurveyed areas	45%	73%	40%	23%	70%	154%	130%	61%

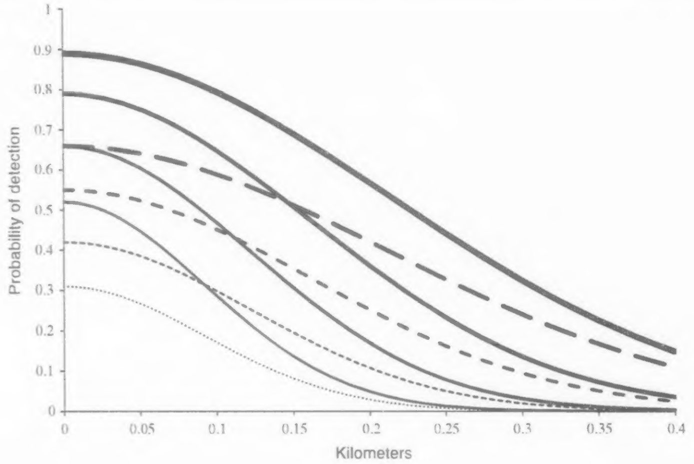

Figure 7

Probability of sighting an available group of harbor porpoise (*Phocoena phocoena*) during the 1997 aerial survey in Southeast Alaska by distance (km) from the survey trackline. Solid lines represent the probability of a sighting when both side observers and a belly observer were present. Thickness of the line (thick to thin) represents visibility codes excellent, good, fair, and poor. Dashed lines represent the probability of a sighting with only side observers (without a belly observer), where long to short dashes represent visibility codes excellent, good, fair, and poor.

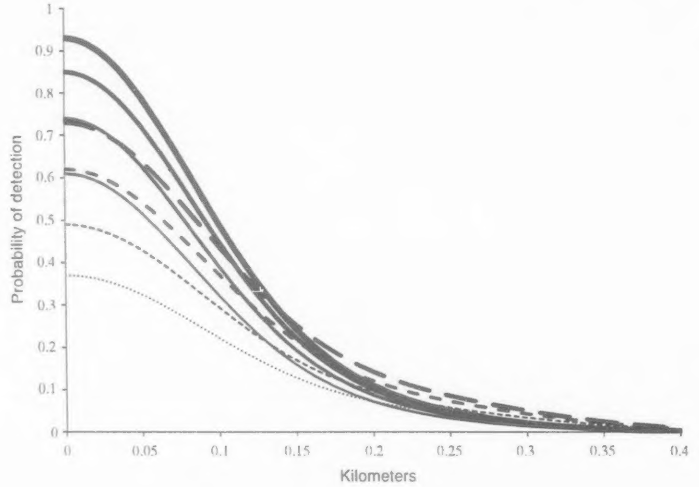

Figure 8

Probability of sighting an available group of harbor porpoise (*Phocoena phocoena*) during the 1998 and 1999 aerial surveys in the Gulf of Alaska and Bering Sea, respectively by distance (km) from the survey trackline. Sighting distributions were sufficiently similar between the two years that a single curve was used for both. Solid lines represent the probability of a sighting when both side observers and a belly observer were present. Thickness of the line (thick to thin) represents visibility codes excellent, good, fair, and poor. Dashed lines represent the probability of a sighting with only side observers (without a belly observer), where long to short dashes represent visibility codes excellent, good, fair, and poor.

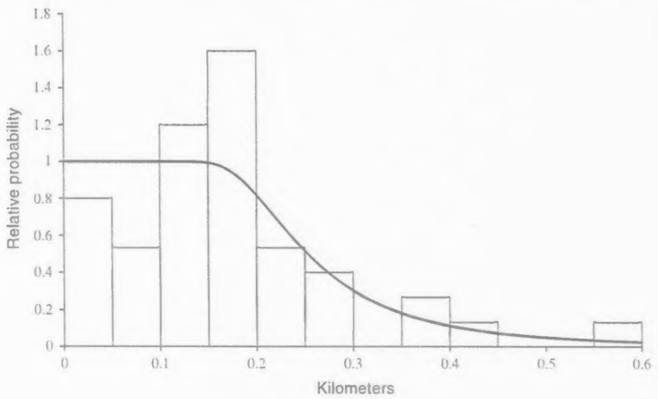

Figure 9

Relative probability of detection by distance from the survey trackline (km) by using a hazard-rate model for the 1998 sighting data for harbor porpoise (*Phocoena phocoena*) in Cook Inlet harbor (relative to 1.0 at zero). The histogram shows the distribution of sightings in 0.05-km groups.

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Appendix I: Errors in species identification

Sightings matched between the side observers and belly observers provided an opportunity to estimate the probabilities that species were misidentified by examining discrepancies in species identification between the matched data. Two types of discrepancies were found: 1) hierarchical discrepancy, where one observer identified the animal (or group) to species while the other observer identified the animal only to genus, family, etc., and 2) mismatched species identification, where two different species were identified. In the case of hierarchical discrepancies, identifications that were not to species could be treated as missed sightings and discarded for the purpose of estimation of species abundance. The mismatched species were of greater concern. There were four possible outcomes when both observers identified the group to the species level: 1) both observers correctly identified the species, 2) one observer was correct and the other was incorrect, 3) both observers were incorrect and disagreed on the species, and 4) both observers were incorrect but agreed on an incorrect identification. From the matched data, types 1 and 4 showed no discrepancy and were thus indistinguishable; types 2 and 3 showed a discrepancy but were also not distinguishable from each other. These discrepancies are assumed to be the result of one of the following: an incorrect identification, an error in reporting by an observer, or a typing error by the data recorder. The errors are assumed to follow a binomial model and to have a generally low probability, so that the likelihood of two errors occurring for the same sighting (outcomes 3 and 4) would be negligible. The following analysis estimates the rates of single errors. Data collected under circumstances with less than 95% reliability for species identification were dropped from the abundance analysis.

The tendency toward errors for species identification can vary by 1) environmental conditions, 2) observer, or 3) recorder. Logistic regression was used to test each of these possible covariates and identify circumstances that were correlated with greater likelihood of discrepancies. A maximum likelihood scheme was then developed to estimate the error rates. Letting p_{ijox} be the probability that an observer o in circumstance x identifies species i as species j, the likelihood (L) that a sighting will be identified as a particular species m is calculated as follows:

$$r_{ai} = R_{ai} \Big/ \sum_i R_{ai},$$

$$L(m,x) = \sum_i r_{ai} p_{imx},$$

where R_{ai} = the actual encounter rate of species i; and
r_{ai} = the fraction of encounters that are species i.

The likelihood of a particular pair of species identifications m and n occurring for a given sighting by one observer in circumstance x and a second observer in circumstance y, is

$$L(m,n,x,y) = \sum_i r_{ai} p_{imx} p_{imy}.$$

In anticipation of a limited data set with a reliability rate greater than 95%, we assumed that outcomes 3 and 4 are rare events compared to outcomes 1 and 2, and therefore we ignored outcomes 3 and 4 in the likelihood model. Second, we assumed that the likelihood of an error is independent of the species involved, and therefore the likelihood is simplified to

$$L(m,n,x,y) \propto \begin{cases} p_x p_y & \text{if } m = n \\ (1-p_x)p_y + (1-p_y)p_x & \text{if } m \neq n \end{cases}.$$

Letting s_{xy} be the number of sighting pairs that occurred under circumstances x and y, and d_{xy} the number of discrepancies in species identification that occurred, the likelihood of a particular set of species identifications was

$$L(S,D,XY) = \prod_{XY} \binom{s_{xy}}{d_{xy}} \left[p_x p_y\right]^{(s_{xy}-d_{xy})}$$
$$\left[(1-p_x)p_y + (1-p_y)p_x\right]^{d_{xy}},$$

where S = the set of matched sightings;
D = the set of species discrepancies within that set; and
XY = the set of circumstance pairs under which matched sightings were made.

Maximum likelihood solutions were found iteratively for each of the covariate sets identified by the logistic regression as correlated with discrepancies. Observers were stratified into inexperienced (no aerial survey experience before this survey and 10 or fewer days on this survey) and experienced (at least one survey season of experience or more than 10 days on this survey), and environmental factors were considered individually. Likelihoods were compared to identify the most likely model and survey effort under circumstances with less than 95% reliability of correct species identification discarded.

Appendix II: Estimation of *g*(0) (which accounts for perception bias only)

Perception bias for a single observer, $P(Y)$, was estimated for effort condition vector Y, as the probability that a group of harbor porpoise available to the observer would be perceived and identified to species by an observer from the logistic regression model as

$$P(Y) = \frac{e^{\beta Y}}{1+e^{\beta Y}},$$

where β = the vector of coefficients estimated in the logistic regression.

Observations from the side observers and belly observer were combined and duplicates removed for density estimation so that the perception bias for the observer team, $P_t(Y_l, Y_b, Y_r)$, (where l, b, and r are the left side, belly, and right side observers, respectively) was the probability that at least one of them would perceive the group. The visual field of the side observers was treated as though their field of view ended at 90° from the horizontal on each side. These observers were in open communication and duplicates were resolved during the survey, so that each observer effectively watched half of the survey trackline. Thus, $g(0)$ for any transect segment with constant environmental conditions was

$$g(0)=1-\left[1-P(Y_b)\right]\left[1-\frac{P(Y_l)+P(Y_r)}{2}\right].$$

Variance was estimated by the delta method as

$$\operatorname{var}(g(0))=\left[D_\beta(Y_l,Y_b,Y_r)^T\,\Sigma_\beta D_\beta(Y_l,Y_b,Y_r)\right],$$

where

$$D_\beta(Y_l,Y_b,Y_r)=\frac{\partial\Gamma_\beta}{\partial\beta}=\frac{1-P_b}{2}$$
$$\left[(y_bP_b+y_lP_l)(1-P_l)+(y_bP_b+y_rP_r)(1-P_r)\right],$$

with Γ_B = the variance-covariance matrix for B estimated during the logistic regression;

D_B = the vector of partial derivatives of P_t with respect to the coefficients (B).

Effects of lunar cycle and fishing operations on longline-caught pelagic fish: fishing performance, capture time, and survival of fish

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Abstract—Commercial longline fishing data were analyzed and experiments were conducted with gear equipped with hook timers and time-depth recorders in the Réunion Island fishery (21°5′S lat., 53°28′E long.) to elucidate direct and indirect effects of the lunar cycle and other operational factors that affect catch rates, catch composition, fish behavior, capture time, and fish survival. Logbook data from 1998 through 2000, comprising 2009 sets, indicated that swordfish (*Xiphias gladius*) catch-per unit of effort (CPUE) increased during the first and last quarter of the lunar phase, whereas albacore (*Thunnus alalunga*) CPUE was highest during the full moon. Swordfish were caught rapidly after the longline was set and, like bigeye tuna (*Thunnus obesus*), they were caught during days characterized by a weak lunar illumination—mainly during low tide. We found a significant but very low influence of chemical lightsticks on CPUE and catch composition. At the time the longline was retrieved, six of the 11 species in the study had >40% survival. Hook timers indicated that only 8.4% of the swordfish were alive after 8 hours of capture, and two shark species (blue shark [*Prionace glauca*] and oceanic whitetip shark [*Carcharhinus longimanus*]) showed a greater resilience to capture: 29.3% and 23.5% were alive after 8 hours, respectively. Our results have implications for current fishing practices and we comment on the possibilities of modifying fishing strategies in order to reduce operational costs, bycatch, loss of target fish at sea, and detrimental impacts on the environment.

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Empirical studies have shown that surface longlines set at night are more productive for capturing swordfish (*Xiphias gladius*) than longlines set during the day (Kume and Joseph, 1969). Studies with ultrasonic telemetry have proved useful for understanding habitat distribution and for providing some insights into short-term horizontal and vertical movements of swordfish (Carey and Robinson, 1981; Carey, 1990). Recently, more advanced tagging technology devices, such as archival tags (Takahashi et al., 2003) and pop-up satellite archival tags (Canese et al., 2008; Neilson et al., 2009), have provided comprehensive information on the diel behavior of swordfish and their movement patterns, both of which indicate the ability of swordfish to navigate to long distance feeding areas in the Pacific and Atlantic oceans and Mediterranean Sea. Vertical movement data obtained from these various studies have shown diel diving patterns to be very consistent, as have been observed in other pelagic fishes (Musyl et al., 2003). During the daytime, swordfish can spend most of their time at depths between 250 and 650 m (Canese et al., 2008) and as deep as 900 m (Takahashi et al., 2003). At crepuscular hours, they swim up and down through a considerable range of depths following the movements of organisms in the deep sound-scattering layers but restrict their movements to forage in the uniform surface mixed-layer during the night. They also feed during the day and can demonstrate basking behavior. Carey and Robinson (1981) suggested that swordfish swimming activity in the water column is closely associated with prey locations and concluded that lunar illumination was a determining factor influencing vertical migrations. Swordfish are "strike and return" feeders (Nakamura, 1983) targeting fast-moving prey. Swordfish can achieve a maximum speed of

130 km/h (Lee et al., 2009) and Fritsches et al. (2005) demonstrated that their large eyes and pupils are ideally adapted to detect rapid movements in dim light. Swordfish rely on visual cues at small scales (meters) and ambient light conditions are likely to be a major factor influencing feeding behavior.

There is strong anecdotal information from captains who target large pelagic fish that the lunar phase affects fishing success for swordfish and other pelagic fish. The effect of the lunar cycle on swordfish catchability has been investigated in longline (Bigelow et al., 1999; Neves Dos Santos and Garcia, 2005; Damalas et al., 2007) and driftnet fisheries (Di Natale and Mangano, 1995), but the results obtained are not directly comparable because they were conducted in different areas and fisheries. Generalized additive models (GAMs) have been used to examine the relative influence of environmental conditions and operational factors on pelagic longline catch rates (Bigelow et al., 1999; Walsh and Kleiber, 2001; Tserpes et al., 2008). In the case of the Réunion Island longline fishery, Guyomard et al. (2004) demonstrated significant effects (among others) of geostrophic currents generated by sea level anomalies (SLA) and lunar day on swordfish catch and catch per unit of effort (CPUE, number of fish per 1000 hooks).

I n 1991, the first swordfish longliner began operating from Réunion Island, a French overseas territory in the southwestern Indian Ocean (21°5′S lat., 53°28′E long.), Two main factors promoted the development of this fishery: 1) the success of the Asian fleet that was based at Réunion Island and 2) a new tax regulation, offering exemption for certain investments in French overseas territory, which encouraged French fishing companies to come to Réunion Island. The annual average catch in the Réunion Island longline fishery during the years 1996–2000 was 2670 metric tons (t) and the composition by weight was 1730 t (65%) of swordfish (*Xiphias gladius*), 320 t (12%) of albacore (*Thunnus alalunga*), 270 t (10%) of yellowfin tuna (*T. albacares*), 130 t (5%) of bigeye tuna (*T. obesus*), 90 t (3%) of billfish (Indo-Pacific black marlin [*Makaira indica*], Indo-Pacific blue marlin [*M. mazara*], shortbill spearfish [*Tetrapturus angustirostris*], and Indo-Pacific sailfish [*Istiophorus platypterus*]), 60 t (2%) of sharks, and 70 t (3%) of other species.

The main goal of the current study was to investigate the performance of the domestic longline fishery at Réunion Island with regard to several variables to determine whether lunar periodicity affected the catch of pelagic species. A three-year logbook data series (1998–2000) was used. In addition, data were augmented by deploying time-depth recorders (TDRs) and hook-time recorders on a number of commercial longline sets. Information on capture time from hook timers allowed us to investigate the survival of large pelagic fish on longlines. Hourly catch rates were correlated with lunar illumination but also with the tidal phase which could be considered as an indicator of induced local currents.

Finally, to test the assumption that feeding behavior of large pelagic fish was predicated on vision (swordfish can differentiate between blue-green wavelengths [Fritsches et al., 2005]), we investigated whether green chemical lightsticks influenced catch rates and species composition. With the combined results for catch rates and species composition, we comment on the possibilities of modifying fishing operations and strategy 1) to reduce operational costs during fishing trips, 2) to reduce loss of target fish at sea, and 3) to reduce bycatch mortality in accordance with the United Nations guidelines for responsible fisheries (FAO, 2003).

Materials and methods

Operational characteristics of the domestic longline fleet

The Réunion Island swordfish longline fishery is a surface fishery. An adapted "American style" gear is used, where the monofilament mainline (3.5–4 mm in diameter) longline is set at dusk and fished during the night. The mainline was deployed from a hydraulically powered spool over the stern and fishing depth was controlled by adjusting branchline (~20 m) and floatline lengths (~10–90m), distance between buoys (~50 m), number of hooks between floats (6–10 hooks), and vessel speed (Fig. 1). In strong currents, lead weights can also be added to branchlines to control mainline depth. The fishery uses J hooks (size 8/0 or 9/0) baited with squid *(Illex* spp.) and green chemical lightsticks were attached ~1 m above the hook on every third branchline.

The domestic longline fleet can be categorized by two vessel sizes (classes): a small-medium boat class (vessels <16 m), and a large boat class (vessels ≥16 m). The fishery underwent dramatic changes between 1992 and 2000 expanding from 5 to 23 active small-medium boats and from zero to 9 large boats, the latter with a peak of 14 in 1998. No longliners were authorized to fish within a zone of 30 nautical miles (~55 km) from Réunion Island in order to avoid conflicts with the artisanal tuna fishery. Thus, these vessels explored new fishing areas within and beyond the French Exclusive Economic Zone (EEZ) (Fig. 2). The number of days at sea varied according to vessel size, vessel capacity, and weather conditions. The smallest boats stayed at sea 2–3 days, medium-size vessels generally stayed 6–8 days; whereas some of the largest vessels stayed at sea for up to 30 days. The large boats gradually expanded to fishing grounds to the west and southwest of Réunion Island within the EEZ in association with deep seamounts and sea surface temperature (SST) fronts (Fig. 2; area C) and to the Mozambique Channel (area B) and to Seychelles Island waters in 1997 and 1998 (area A). A decline of large boats from the fleet brought notable changes; therefore catches in 1999 and in 2000 were taken mainly around Réunion Island between 20° and 25°S lat. and 50°–60°E long. Only a few vessels ventured far from Réunion Island in 2000. Table 1 summarizes

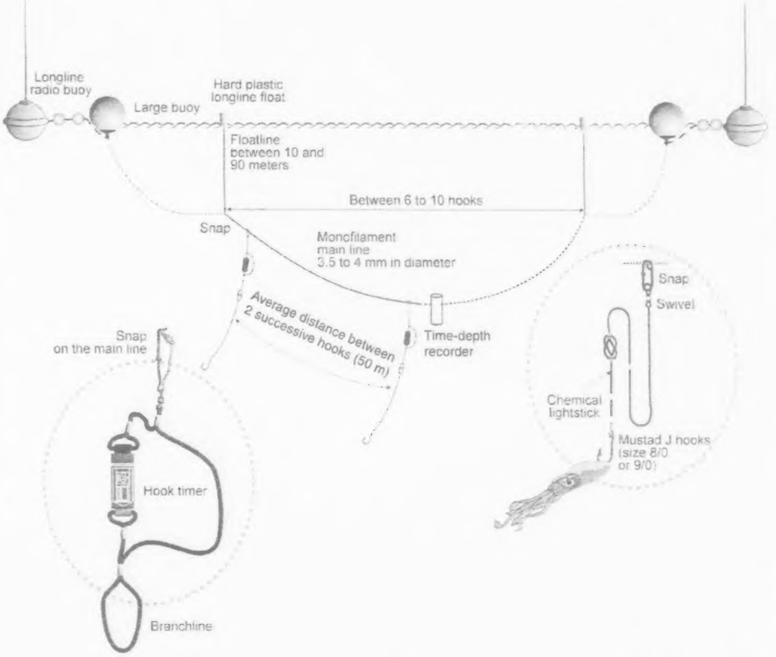
Longline radio buoy
Large buoy
Hard plastic longline float
Floatline between 10 and 90 meters
Between 6 to 10 hooks
Snap
Monofilament main line 3.5 to 4 mm in diameter
Average distance between 2 successive hooks (50 m)
Time-depth recorder
Snap on the main line
Hook timer
Branchline
Snap
Swivel
Chemical lightstick
Mustad J hooks (size 8/0 or 9/0)

Figure 1

Longline gear used in the domestic Réunion Island longline fishery: hook timers, time-depth recorders, and chemical lightsticks. Experiments were conducted off the island between June 1998 and November 2000.

the fishery and environmental indices and subsequent statistical analyses.

Logbook (database 1)

During the "Programme Palangre Réunion" (PPR), a rigorous data-collecting strategy was implemented. Logbooks were distributed to all domestic vessels, along with species identification guides, including guides for identifying sharks and sea turtles. Because these logbooks were completed on a voluntary basis, logbook data were cross checked against landing receipts to estimate the monthly logbook coverage. Logbook data made up the major source of information used to analyze the effect of operational and gear-setting practices on catches.

Analyses focused on data collected between 1998 and 2000 and which encompassed several lunar cycles. Logbook submission was high by the domestic fleet and the fleet operated between 20° and 23°S lat. and 53° and 57° long. (Fig. 2, area D). Database 1 consisted of 2009 longline sets where seven species were easily identified: albacore, bigeye and yellowfin tuna, dolphinfish, swordfish, blue (*Prionace glauca*) and oceanic whitetip sharks (*Carcharhinus longimanus*), and three broader shark species groups (mako sharks [*Isurus* spp.], hammerhead sharks [*Sphyrna* spp.], and other sharks grouped together as "mixed sharks").

Experimental fishing (databases 2 and 3)

Fish behavior on a daily scale (fine scale) was investigated on portions of the longlines equipped with hook timers to estimate fish capture time and with time-depth recorders (TDRs) attached in the middle position between two consecutive floats, which is theoretically the deepest point reached by the mainline. On 160 sets, 284 TDRs were used to estimate hook depth (TDR depth+branchline length). The number of hook timers deployed per set varied from 61 to 408 according to the boat size and weather conditions. For thirty-three trips, 28,974 hook timers were used during 160 sets. These experimental data constituted database 2. The time between the setting of the hook and capture time was represented as a capture index and stratified into four classes (0–4 h, 4–7 h, 7–10 h and >10 h). Database 3 represented other longline field trials where CPUE and catch compositions were compared by using gear with various densities of chemical lightsticks.

Environment (database 4)

Database 4 consisted of two environmental databases that were linked to experimental databases to investigate cyclical lunar influence on CPUE. Lunar days were coded in chronological order with values between 1 and 30. A lunar phase index was allocated to each fishing day according to the four phases of the moon (new moon, first quarter, full moon, and last quarter). Full and new moons refer to the day of each full or new moon ±2 days. Lunar illumination was calculated for each fish caught, according to its hooking hour, based on the angle of elevation of the moon (on a 24-h cycle). These data were obtained by using an astronomical software package called LunarPhase (http://www.nightskyobserver.com/LunarPhase/index.htm, accessed January 2000) and were stratified into three classes: 1) angle <45° (low illumination); 2) high illumination (angle >45°–90°); and 3) dark (new moon). An important underlying assumption inherent in this approach is that the cloud coverage is not considered when calculating the index. An index for tidal phase was assigned to each hooking time and location by the French Service Hydrographique et Oceanographique de la Marine (SHOM). The tidal index consisted of four nominal phases (ebb, high, flood, and low) and is thus a good approximation of the theoretical sea level height changes, although it does not account for current velocity. The fishery operates throughout the year and no temporal discontinuities in fishing effort were evident because effort was quite homogeneous for indices of lunar illumination and tide phase.

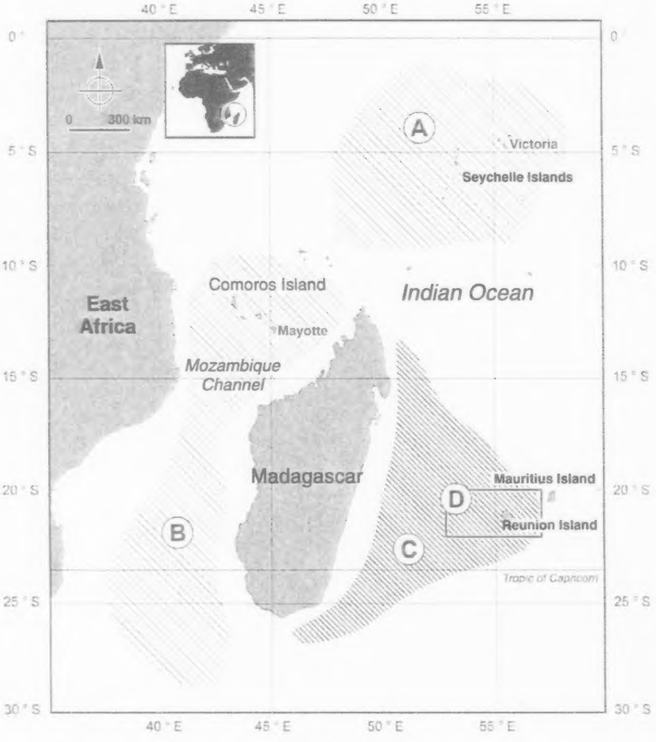

Figure 2

Location of Réunion Island in the southwestern Indian Ocean. The areas shown with diagonal lines are the three fishing grounds of the fleet between 1998 and 2000, the Seychelle waters (area A), the Mozambique Channel (area B), the west and southwest of Réunion Island within the EEZ in association with deep seamounts and sea surface temperature (SST) fronts (area C). Logbook data used to analyse the effect of operational and gear setting practices on catches where located in area D (20°–23°S lat. and 53°–57°E long.)

Statistical methods

Lunar effect on fishing performance was investigated at two different scales. At a larger scale, we conducted a between-class analysis (Dolédec and Chessel, 1990, 1994; Gaertner et al., 2005; Bigot et al., 2008) in order to approximate the influence of lunar days (phase) on the CPUE of all the species recorded in logbooks (database 1), where "lunar days" was a categorical factor. For that purpose, we sought axes for the between-group analysis that would best discriminate the centers of gravity of each lunar day and allow us to investigate associations between lunar phases and the variability of CPUE for each species. In addition, a permutation test, which extended the test of Romesburg (1985) to all kinds of variables (Manly, 1991), was carried out to test the significance of the between-group variability. We used nonparametric LOESS regression to further investigate variability in CPUE for species that were most affected by the lunar day. On a finer scale, we carried out a multiple correspondence analysis (MCA)—equivalent to normalized principal component analysis (PCA) to determine the most favourable catch factors on a daily scale (Tenenhaus and Young, 1985; Mazouni et al., 1996). MCA allowed us to visualize the associations between each of the five major species caught during experimental sets and three lunar-related factors studied on a daily scale (tide phase, capture time, lunar illumination).

A between-group centered principal component analysis (CPCA, R-mode) and a between-group factorial correspondence analysis (FCA) were conducted to examine the influence of lightstick density on CPUE and catch composition of experimental sets (database 3). The ADE-4 software (Thioulouse et al., 1997, http//pbil.

Table 1

Variables, indices, and types of analyses performed during our study to elucidate the direct and indirect effects of lunar cycle and other operational factors affecting fishing performance, fish behavior, capture time, and fish survival for the domestic Réunion Island longline fishery.

Database	Scale	Variable	Index	Type of analyses
1 Logbook	Set (day)	Number of fish (7 species, 3 broad groups) number of hooks	CPUE (number of fish per 1000 hooks)	Between classes analysis, Permutation test, Nonparametric loess regression
2 Experiments with hook timers (HT)	Hook (hour)	Setting time Capture time	Elapsed time after setting as capture time index (0–4 h, 4–7 h, 7–10 h, and >10 h)	Multiple correspondence analysis
3 Experiments with lightsticks	Set (day)	Number of fish (7 species, 3 broad groups) Number of hooks Lightstick density	Lightstick density and CPUE	Centered principal component analysis (CPCA)
			Catch composition (percentage of fish per species	Factorial correspondence analysis (FCA)
4 Environmental	Set (day)	Lunar day	Lunar day (1 to 30) and lunar phase index (new moon, first quarter, full moon, last quarter)	
	Hook (hour)	Angle of elevation of the moon tide characteristics	Lunar illumination index: low illumination intensity (angle <45°), high illumination intensity angle (45°–90°) and dark (new moon)	
			Tide phase index (ebb, high, flood and low)	

univ-lyon1.fr/ADE-4, accessed January 2000) was used to perform calculations and graphical displays for between-group analyses.

Results

Effect of the moon at a large scale

Time series covered by logbook data The CPCA indicated that lunar day represented only 13.3% of the total variability, although the influence of the lunar day on CPUE was highly significant (permutation test, $P<0.01$). The first two axes explained 71% and 17% of the between-lunar-day variability and illustrated the effect of lunar days on CPUE (Fig. 3). Albacore CPUE reached maximum values during the full moon (between the 13th and 19th day of the lunar cycle), whereas CPUE was less important during the new moon (between the 25th and 6th day of the lunar cycle).

Swordfish was the unique component of the second axis (Fig. 3) and the projection of lunar days on this axis indicated that the highest CPUE occurred mainly during two short periods of time within the lunar cycle, between the 7th and 9th day and between the 23rd and 26th day. None of the other four species analyzed appeared to be affected by the lunar day (Fig. 3).

Case study of albacore and swordfish For albacore, LOESS regression confirmed that the highest CPUE was obtained during the full moon (Fig. 4A). In contrast, there was no apparent influence of tidal fluctuation (Fig. 4C). The situation for swordfish was more complex. Variation of CPUE according to lunar cycle provided less contrast than that for albacore. LOESS regression confirmed that the highest CPUE was obtained during the first and last quarter of the moon as characterized by the lowest tidal ranges. Nevertheless, the relationship between swordfish CPUE and lunar intensity was not consistent because the CPUE progressively decreased during the last days of the last quarter and reached the lowest values around the full moon phase (Fig. 4B). Moreover, CPUE decreased as tidal amplitude increased. Large confidence intervals around the mean CPUE pertaining to the new moon indicated a higher variability in fishing performance during this phase. The lowest CPUE was recorded between the 14th and 17th day of the lunar cycle during the full moon (which is characterized by the largest tidal ranges and maximum lunar illumination).

Effect of lunar luminescence, tidal phase, and tidal velocity of local induced currents on catches

Sample sizes of five species were considered adequate to conduct detailed analyses of lunar-related variables on a fine scale, although 15 species and 2 broader species groups were identified in the catches (Table 2). Swordfish were caught rapidly after the gear was set (Fig. 5) and during days characterized by weak lunar illumination because most of the individuals were confined in an area corresponding simultaneously to the negative part of both axes (Fig. 6). The occurrence of swordfish on the negative side of the first axis and mainly on the negative axis of the second axis indicates that swordfish were caught during low tides and to a lesser extent during flood tides characterized by a low current. These results reinforce earlier conclusions obtained at a large scale, although the results from the experimental data were weaker than the data from logbooks.

As with swordfish, bigeye tuna are likely to be caught rapidly after the gear is set during periods of weak lunar illumination (Figs. 5 and 6). Bigeye tuna and blue shark exhibited an opposite distribution on the second axis, which indicated that blue sharks were caught late during the soak time of the longline set and when luminescence was minimal. The limited number of albacore and yellowfin caught in the experimental data may have restricted the statistical analysis. No particular favorable or unfavorable conditions were identified for albacore on a daily scale (Fig. 6), in contrast to the influence of lunar intensity observed on a monthly scale.

Effect of chemical lightsticks

A marginally significant influence of lightstick density on CPUE and catch composition was observed (permutation tests, $P<0.05$); but the majority of the CPUE variability was not correlated with lightstick density (93.6% for PCA and 91.3% for FCA, Table 3).

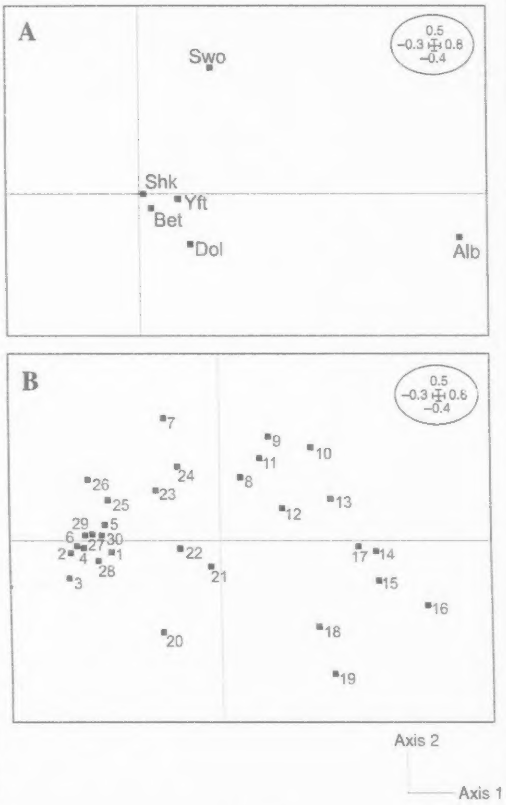

Figure 3

A between-group projection of (**A**) the species, and of (**B**) the lunar days of the month (represented as numbers between 1 to 30), on the first plane of the between-group centered principal component analysis (CPCA) conducted on catch per unit of effort of albacore (Alb, *Thunnus alalunga*); swordfish (Swo; *Xiphias gladius*); bigeye tuna (Bet, *Thunnus obesus*); yellowfin tuna (Yft, *Thunnus albacares*); sharks (Shk), and dolphinfish (Dol, *Coryphaena hippurus*). Scale box in the upper right corner of each plot indicates the limits for the first and second axes.

Capture depths, times, and fish survival

TDRs indicated that the deepest depth of the mainline was 110 m; most of the longlines were deployed between 30 and 110 meters (Fig. 7); consequently most hooks fished between 50 and 130 meters. Hook timers indicated that the number of commercial species caught (swordfish and tunas) declined with soak time (i.e., with the time the gear was in the water [Fig. 5A]) and indicated an opposite trend for five bycatch species (Fig. 5B). Blue marlin and dolphinfish were mostly caught after the longline had soaked for 8 hours or longer. In particular, pelagic stingrays, and sailfish to a lesser extent, were caught mostly during gear retrieval. In contrast, more than 60% of the sharks were caught within the initial seven hours of fishing.

Fish survival at longline retrieval varied widely among species (Table 4). Survival was high for species such as dolphinfish and black marlin which strike the hooks mainly during retrieval. Over 40% of the main elasmobranch species (blue shark, oceanic whitetip, and pelagic stingray), as well as sailfish, were alive upon retrieval. Among commercially important species, 49% of the bigeye tuna were alive upon retrieval, whereas only 3 of 79 albacore were alive. Swordfish survival was also low (20%) and no relationship was evident between fish size and mortality. Bigeye tuna and two shark species exhibited the highest survival when the longline was at a settled depth. Six species (represented by sample sizes >30 individuals) exhibited long survival times of up to 14 hours after capture (Table 4).

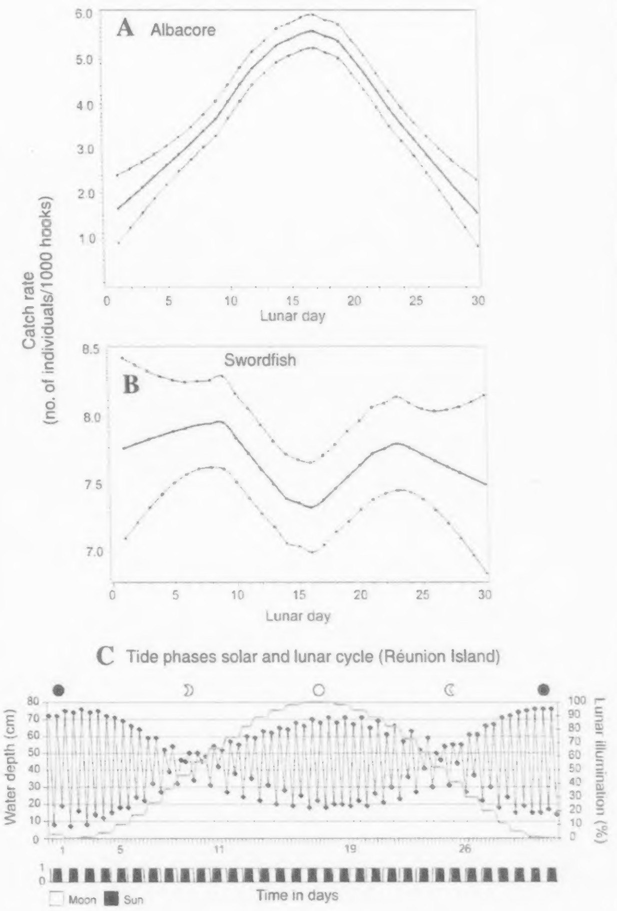

Figure 4

Variation of the mean catch per unit of effort (and 95% confidence intervals) of (**A**) albacore (*Thunnus alalunga*), and (**B**) swordfish (*Xiphias gladius*) per lunar day determined with a nonparametric regression method (LOESS) between 1998 and 2000. Tidal ranges and lunar luminescence during a complete lunar cycle are illustrated in (**C**).

Discussion

Lunar illumination and sensory abilities of large pelagic fish

At a broad scale, our results indicate that the phases of the moon, which presumably affect ambient light levels, have a significant but limited influence on the night catch rates of albacore and swordfish in the Réunion Island-based swordfish longline fishery, whereas such a lunar influence was not found for other species. We found that the highest swordfish CPUE occurred during the first and last quarters of the lunar cycle—a finding that is consistent with the results obtained for the same fishery in the Indian Ocean (Guyomard et al., 2004).

Other studies conducted in various geographical areas with distinctive oceanic features, have indicated that lunar influences on swordfish CPUE are not consistent. The highest swordfish CPUE occurred during the full moon phase in the Hawaii-based swordfish fishery (Bigelow et al., 1999) and in the central Atlantic swordfish fishery (Draganik and Cholyst, 1988). In the U.S. longline fishery in the western Atlantic, more hooks were deployed in the 2-week period around full moon, but Podesta et al. (1993) could not demonstrate a significant correlation between CPUE and lunar illumination, whereas Hazin et al. (2002) and Damalas et al. (2007) showed positive effects of other lunar phases on swordfish CPUE. No significant relationship between lunar phase and swordfish abundance could be demonstrated in artisanal swordfish fisheries off the Cuban coast (Moreno et al., 1991). In the case of a swordfish gillnet fishery operating in the Mediterranean Sea, Di Natale and Mangano (1995) showed that the lowest catch rate occurred during the full moon. Lastly, it is apparent that swordfish size and maturity may confound catch rates during different lunar phases (Draganik and Cholyst, 1988; Neves Dos Santos and Garcia, 2005).

One possible explanation for the absence of a consistent pattern in association with lunar phase could be attributed to prey availability. In the Atlantic Ocean, swordfish appear to exhibit feeding plasticity (i.e., are opportunistic feeders and exhibit various search strategies for prey) based on forage abundance and prey size; larger swordfish tend to eat larger prey than smaller swordfish (Chancollon et al., 2006). In the Pacific Ocean, Young et al. (2006) showed no significant relation-

Table 2

Number and percentage of catch per species during experimental sets conducted from commercial vessels in the domestic Réunion Island-based longline fishery between June 1998 and November 2000.

Common name	Species	Number of individuals	Percentage
Swordfish	*Xiphias gladius*	389	47.8
Blue shark	*Prionace glauca*	92	11.3
Bigeye tuna	*Thunnus obesus*	86	10.6
Albacore	*Thunnus alalunga*	79	9.7
Yellowfin tuna	*Thunnus albacares*	66	8.1
Common dolphinfish	*Coryphaena hippurus*	48	5.9
Oceanic whitetip shark	*Carcharhinus longimanus*	17	2.1
Pelagic stingray	*Pteroplatytrygon violacea*	12	1.5
Indo-Pacific sailfish	*Istiophorus platypterus*	7	0.9
Hammerhead sharks	*Sphyrna* spp.	4	0.5
Indo-Pacific black marlin	*Makaira indica*	3	0.4
Escolar	*Lepidocybium flavobrunneum*	3	0.4
Indo-Pacific blue marlin	*Makaira mazara*	2	0.2
Wahoo	*Acanthocybium solandri*	2	0.2
Shortfin mako shark	*Isurus oxyrinchus*	2	0.2
Barracuda	*Sphyraena* spp.	1	0.1
Leatherback turtle	*Dermochelys coriacea*	1	0.1
Total hook timers triggered		2115	
Hook timers triggered with catch		814	
Hook timers triggered without catch		1301	

ship between prey biomass and lunar phase but found that prey size significantly increased with swordfish size and that this increase coincided with a dietary shift from fish to cephalopods (Palko et al., 1981). This finding indicates that swordfish have the ability to forage at considerable depth and temperature, which are afforded by a suite of physiological adaptations to enable opportunistic feeding within the deep sound-scattering layer (DSL) (Josse et al., 1999; Musyl et al., 2003), Gilly et al. (2006) depicted lunar influence on the vertical migration of squid, which, in turn, would have a direct effect on the distribution and vulnerability of swordfish.

Table 3

Decomposition of inertia between and within groups according to the lightstick density factor for centered principal component analysis (CPCA), factorial correspondence analysis (FCA), and associated permutation tests.

	Between lightstick density CPCA	Between lightstick density AFC
Total inertia	$3.234\ 10^{2}$	1.597
Between groups	$2.046\ 10^{1}$ (6.32%)	$1.391\ 10^{-1}$ (8.7%)
Within groups	$3.030\ 10^{2}$ (93.68%)	1.458 (91.3%)
Permutation test	$P<0.05$	$P<0.05$

We found that higher swordfish CPUE correlated with small tides. Moreover, at a finer scale, we found that higher swordfish CPUE occurred with lower tidal fluctuations which coincided with the possible generation of low-velocity oceanic currents. These results were consistent with the results obtained when applying GAMs on similar scales (Guyomard et al., 2004), where the meridional component (V) of geostrophic currents derived from sea level anomaly (SLA) data was the most significant environmental factor within one of the models tested. It was likely that the low positive V values (i.e., low velocity currents to the north) were more beneficial for catch rates, whereas the trend became clearly negative for higher velocity values.

We assumed that the influence of the tide and associated local current velocities would be complex and affect the dispersion of organisms within the DSL and other associated organisms of the mixed layer. In addition, current could affect turbidity by advecting organisms and particulate matter and alter the shape and depth obtained by the longline (Bigelow et al., 2006). To gain insights into swordfish behavior during complex patterns of current velocities, acoustic telemetry could be used to provide short-term horizontal movement data that could help in elucidating the effect of the tide on the foraging behavior of large pelagic fish. Analysis

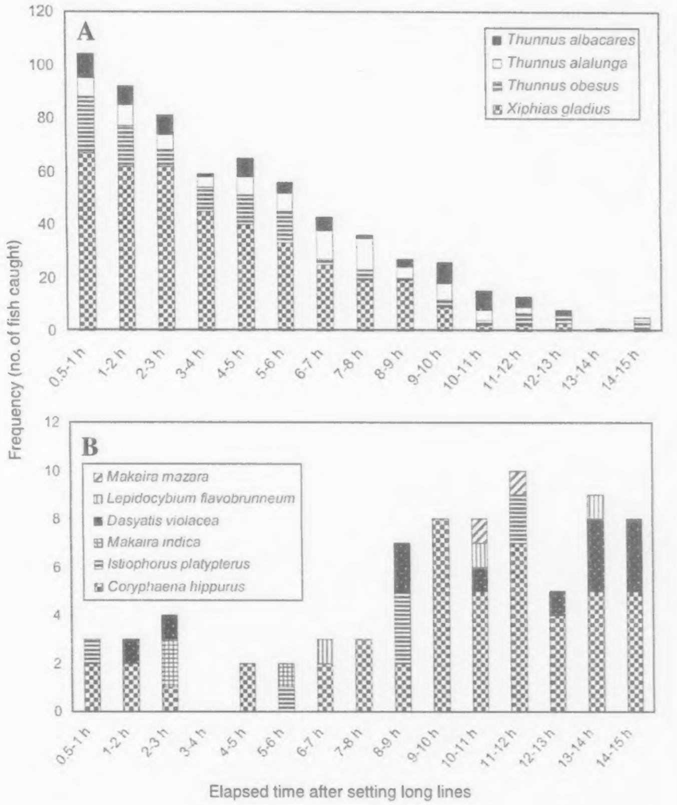

Figure 5

Hook-timer data for 10 species caught on longlines (n=284) in the domestic Réunion Island fishery between June 1998 and November 2000. Height of each bar represents the sum of frequencies for (**A**) the main commercial species and for (**B**) billfish and other bycatch species.

of the trajectories on a finer scale would help in elucidating the foraging behavior in three dimensions. Thus, using acoustic tracks, Brill et al. (1993) presented evidence for passive, current-borne movements (which tended to drift in the prevailing current) for striped marlin around the Island of Hawaii.

Our results revealed that swordfish were caught on days characterized by a weak lunar illumination. It is likely that increased illumination may alter the diving behavior of swordfish in near-surface waters. Ortega-Garcia et al. (2008) stated that vulnerability to gillnets was reduced because of better visibility during the full moon phase whereby swordfish could presumably detect and therefore avoid the net. As a logical extension, we could hypothesize that this visual avoidance could also apply to longline gear. In constrast, albacore exhibited higher CPUE during the full moon, which indicates increased foraging during the time of prey availability. This result supports that of Pusineri et al. (2008), who found that the composition of the diet of pelagic predators in the northeast Atlantic differs considerably in terms of species composition and prey size.

Blue shark, the major shark found in bycatch of tuna and swordfish longline fisheries worldwide (Bonfil, 1994; Gilman et al., 2008) exhibited catch rates that correlated strongly with soak time but were not significantly influenced by lunar effects. To our knowledge, studies of the possible effect of lunar illumination on CPUE are rare for blue shark and virtually nonexistent for albacore and yellowfin tuna because these species are mainly caught during the day by Asian distant-water longline fleets. Our results agree with those of Bigelow et al. (1999), who showed that the effect of the moon phase appeared insignificant on blue shark CPUE. Blue shark are opportunistic feeders that are probably at-

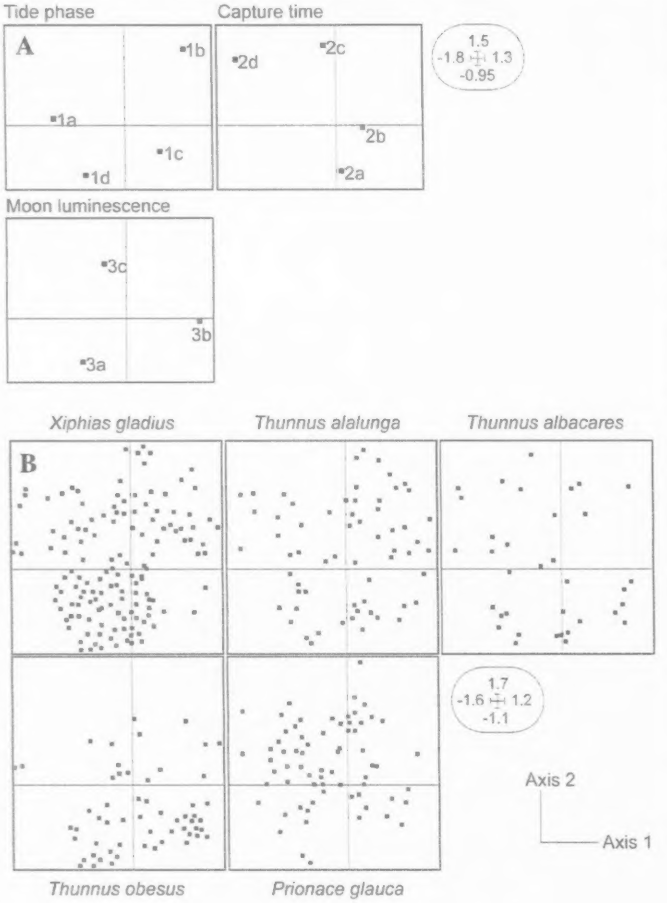

Figure 6

(**A**) Projection of the modalities for each factor on all species combined, and (**B**) the projection of individual fish stratified by species on the first axis of the multiple correspondence analyses (MCA). Description of the index modalities: "tide phase" 1a=ebb; 1b=high, 1c=flood, and 1d=low; "capture time" 2a=0–4 h, 2b=4–7 h, 2c=7–10 h, and 2d=>10 h; "moon luminescence index" 3a=low, 3b=high, and 3c=dark

tracted by offal and spent bait discarded during the haul but also by the distress signals of captured fish (Myrberg et al., 1969)

Our results indicate that swordfish and bigeye tuna exhibit active predation when lunar illumination is weak. These results are consistent with the findings of Fristches et al. (2005), who showed that retinas of swordfish and bigeye tuna provide visual acuity and sensitivity to blue-green light and thus these apex predators are efficient visual hunters in dim light.

We found that 60% to 80% of swordfish were caught after the gear soaked 4–6 hours and these results indicated a possible positive effect of bait freshness on the attractiveness of bait to swordfish and bigeye tuna. The effect of the chemical lightsticks on catch rate also decreased with time and as their glowing intensity waned. The role of the lightsticks is still not clear, although it is thought that they either attract predators to the bait or they attract small fish and squid (Hazin et al., 2005), or both, and as such, were considered as an important refinement of the longline gear. A significant but low association of lightstick density on CPUE was confirmed by our analyses. Bigelow et al. (1999) found that increasing the proportion of lightsticks from

Table 4

Number of fish caught per species (No.), number of fish alive at time of hauling (*no.*), range of size per species (lower jaw fork length for billfish and swordfish, and fork length for other species in cm), maximum survival time per species, percentage of individuals alive at time of hauling, and percentage alive eight hours after hooking.

Common name	Species	No.	*no.*	Length (cm)	Maximum survival time (hours)	Alive at time of hauling (%)	Alive after 8 hours (%)
Swordfish	*Xiphias gladius*	389	76	93–242	14	19.5	8.4
Bigeye tuna	*Thunnus obesus*	86	42	65–160	14	48.8	26.7
Albacore	*Thunnus alalunga*	79	3	105–113	8	3.8	1.2
Yellowfin tuna	*Thunnus albacares*	66	23	99–150	14	34.8	13.6
Common dolphinfish	*Coryphaena hippurus*	48	32	83–120	14	66.7	8.3
Oceanic whitetip shark	*Carcharhinus longimanus*	17	7	120–151	14	41.1	23.5
Blue shark	*Prionace glauca*	92	45	150–240	14	48.9	29.3
Indo-Pacific sailfish	*Istiophorus platypterus*	7	3	?–163	4	42.8	—
Indo-Pacific black marlin	*Makaira indica*	3	3	238–240	2	100	—
Indo-Pacific blue marlin	*Makaira mazara*	2	0	—	—	0	—
Pelagic stingray	*Pteroplatytrygon violacea*	12	5	—	2	41.2	—

0% to 40% on the hooks increased CPUE, but that the effect was not increased beyond this threshold. In contrast, blue shark had an increase in CPUE when the proportion of lightsticks was increased. Beyond an interest in understanding the influence of lunar periodicity and operational factors on the behavior of large pelagic fishes, these potential mechanisms are also of interest to fishermen, and our results also have implications for current and future fishing practices.

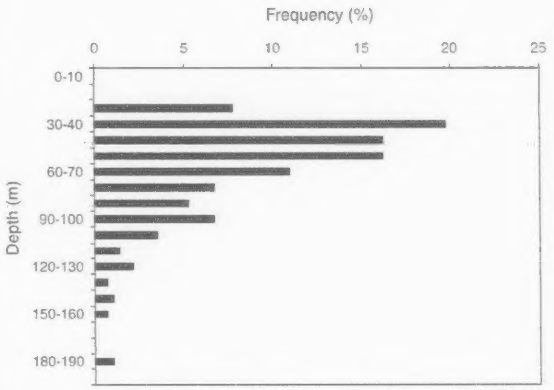

Figure 7

Pooled data from the time-depth recorders located on the mainline in the middle position between two consecutive floats during experimental sets (n=284) in the domestic Réunion Island longline fishery.

Adjustments of fishing strategy and future research needs

This study may help fishermen to modify fishing operations and select a fishing strategy to increase economic benefits and reduce the impact of bycatch mortality. Captains would be able to switch fishing practices to target one species or another according to lunar phase. Moreover, shifting from expensive squid to cheaper mackerel bait to catch albacore could reduce the operational costs during trips in October and November when albacore CPUE is seasonally highest.

We suggest that shortening the soak time during the fishing operation should be beneficial because the major portion of the catch occurred in the first few hours of the operation (presumably bait decreases in quality with time and there is an increase in bait loss) (Lokkeborg and Pina, 1997). Hook-timers and direct observations indicated that swordfish could escape for several hours after capture. Many triggered hook-timers were retrieved without a fish (1301 cases) and they may have been triggered for a variety of reasons, such as being triggered during deployment or retrieval operations, being activated by squids, or may have been triggered by the escape of fishes or turtles. Although we cannot assume that high escape rates have occurred, we had the opportunity to film a swordfish escaping during the hauling of the gear. It succeeded in unhooking itself at the surface but sank immediately from exhaustion. Therefore, even if the fate of the escaped animal was unknown, we assumed that a large proportion of swordfish might die from ingestion of the J hooks. In addition, long soaking periods in warm temperatures increase the degradation of flesh, reducing the market price of the fish. Shortening the soaking time could reduce the chance of depredation by large marine mammals (e.g., false killer whale [*Pseudorca crassidens*], shortfin pilot whale [*Globicephala macrorhyncus*]) and sharks on longline-caught fish. In the United States, limits on the length of a pelagic longline set have been proposed as a management measure to reduce bycatch (Kerstetter, 2008). It has been demonstrated that such a restriction would reduce the interaction rate of longlines with marine mammals in the Mid-Atlantic Bight by approximately 26%.[1]

The survival rates for blue shark and oceanic whitetip shark were estimated to be 49% and 41%, respectively. The survival rate of blue shark at haulback after a soak during the night was lower than that during day longline sets: 100% (Boggs, 1992), 80–90% (Campana et al., 2005), 69% (Diaz and Serafy, 2005), and 87% (Francis et al., 2001). Differences in survival rates among studies may result from hook types, leader material (monofilament or wire), and handling procedures, although survival rates between day and night longlining should be further investigated. Nevertheless, reducing the soaking period would increase the number of sharks released alive. The release of live bycaught sharks (Moyes et al., 2006) and billfish (Kerstetter and Graves, 2006, 2008) is by far the best management measure to reduce longline fishing mortality of these species.

From a cost benefit perspective, fishermen believe that chemical lightsticks improve fishing performance but they limit the number deployed because of the price. However, our data strongly indicate that the use of lightsticks did not increase swordfish catch by very much. Lightsticks are suspected to attract sea turtles to the vicinity of longlines (Wang et al., 2007) and thus may increase their incidental catch; however, lightsticks have a limited lifespan and are not reusable and thus are an environmental concern. Thousands of spent lightsticks are discarded at sea and constitute a potential toxicant to marine flora and fauna. In the case of Réunion Island, local fishermen were keen to retain used chemical lightsticks onboard, store them during the fishing trip, and offload them when returning to port after a significant awareness campaign about the negative environmental impact of lightsticks. In light of our results and for ecological concerns (Ivar do Sul et al., 2009; Pinho et al., 2009), the use of chemical lightsticks should be reconsidered. Recently, the working group of the General Fisheries Commission for the Mediterranean (GFCM) has proposed a ban on chemical lightsticks and any light source in the pelagic longline fishery in the Mediterranean Sea.[2]

Complementary three-dimensional acoustic telemetry experiments are needed to better understand the movements of swordfish and to test the hypothesis that tidal and oceanic currents may influence their foraging behavior and fishing operations associated with their foraging behavior. We also recommend additional studies to understand the interaction of lunar luminescence and swordfish size because of concerns for the sustainability of swordfish stocks and for the protection of certain age classes (Poisson and Fauvel, 2009).

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Using experiments and expert judgment to model catchability of Pacific rockfishes in trawl surveys, with application to bocaccio (*Sebastes paucispinis*) off British Columbia

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Abstract—The time series of abundance indices for many groundfish populations, as determined from trawl surveys, are often imprecise and short, causing stock assessment estimates of abundance to be imprecise. To improve precision, prior probability distributions (priors) have been developed for parameters in stock assessment models by using meta-analysis, expert judgment on catchability, and empirically based modeling. This article presents a synthetic approach for formulating priors for rockfish trawl survey catchability (q_{gross}). A multivariate prior for q_{gross} for different surveys is formulated by using 1) a correction factor for bias in estimating fish density between trawlable and untrawlable areas, 2) expert judgment on trawl net catchability, 3) observations from trawl survey experiments, and 4) data on the fraction of population biomass in each of the areas surveyed. The method is illustrated by using bocaccio (*Sebastes paucipinis*) in British Columbia. Results indicate that expert judgment can be updated markedly by observing the catch-rate ratio from different trawl gears in the same areas. The marginal priors for q_{gross} are consistent with empirical estimates obtained by fitting a stock assessment model to the survey data under a noninformative prior for q_{gross}. Despite high prior uncertainty (prior coefficients of variation ≥ 0.8) and high prior correlation between q_{gross}, the prior for q_{gross} still enhances the precision of key stock assessment quantities.

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Rockfishes (*Sebastes* spp.) are a group of groundfish species on the west coast of North America, many of which are commonly exploited; over 25 stocks are assessed and individually managed in the United States and Canada (DFO, 2008; NPFMC, 2008; PFMC, 2008). Stock assessment models for rockfish are typically fitted to a variety of data, such as estimates of population biomass determined from survey trawl-swept areas. These swept-area biomass estimates are usually treated as relative indices of abundance because of the unknown relationship between the availability of the target population to the survey net. Factors affecting this relationship include the proportion of fish present within the path of the net that on average enter the net, the proportion of the population that is potentially available to be captured by the survey gear and the relative density of rockfish in trawlable and untrawlable areas. Treated as a relative abundance index, a single scalar parameter is typically estimated, called "bulk catchability" or "q_{gross}" to scale the model-predicted population biomass to the swept-area biomass values (Millar and Methot, 2002). Owing to the trawl survey data being available for only a portion of the history of a stock's exploitation and because of moderate to large amounts of variation in interannual error, stock assessment estimates of q_{gross} are often imprecise and may not provide reliable estimates of population biomass (Millar and Methot, 2002).

In order to reduce the large uncertainty common to estimates of q_{gross} and population abundance for rockfishes and many other assessed fishes, stock assessment scientists have quantified Bayesian prior probability density functions (pdfs) for q_{gross}. Among these quantifications, there have been efforts to quantify expert judgment (e.g., Punt et al., 1993; McAllister and Ianelli, 1997; Boyer et al., 2001) on factors affecting survey catchability. Others have performed hierarchical analyses of stock assessments for different rockfish species to quantify the mean and variance in q_{gross} across different populations for surveys, using the same gear (Millar and Methot, 2002). Although these analyses have improved the conceptual understanding of the processes contributing to trawl catchability during surveys and have shown how expert judgment and other information can be used to help form priors, no unifying framework exists that integrates the judgment from multiple experts with other available data on survey catchability.

In this article, we present a synthetic approach for integrating inputs on technical parameters elicited from experts and survey data not used in a stock assessment to form a prior for q_{gross} that can be used to improve the value of biomass estimates from trawl-swept areas for use in stock assessments. This approach can be applied to swept-area abundance estimates across a number of areas and over multiple types of trawl gear (e.g., shrimp and groundfish trawl nets). Each expert is assigned equal prior weight which is then updated from ratios of relative catch rates between different survey gear types. We use estimates of the fraction of the total population biomass that lies within the boundaries of each survey area and that accounts for the fraction of the area within the boundary of each survey that is trawlable. A factor is applied to prevent the expert inputs from being overly certain. Finally, because this method is applied to different surveys of the same stock, these parameters are not independent (in some surveys the same gears were used) and there is spatial covariance in estimates of the fraction of biomass in the different survey areas (the prior pdf formed accounts for the correlations in the q_{gross} parameters between surveys). We illustrate the method with an application to bocaccio (*Sebastes paucispinis*) off British Columbia (B.C.) that relied upon technical information obtained from interviews with a dozen trawl captains. We show the sensitivity of the results to assumptions about potential differences in rockfish density between trawlable and untrawlable substrates, the amount of uncertainty in expert inputs, and how results from different experts should be integrated. The impact on the overall stock assessment results are illustrated by comparing results obtained with and without informative priors for q_{gross}.

Bocaccio in British Columbia were chosen to illustrate the new method to formulate a prior for q_{gross} because this species presents an instance in which the time series of abundance indexes available for stock assessment are mostly too short or imprecise to enable estimation of parameters of population dynamics and abundance trends. An informative prior for survey q is essential to achieve these ends. Bocaccio range from the Alaska Peninsula to Baja California (Love et al., 2002). In British Columbia, adult bocaccio exhibit a widespread distribution mainly on the outer coast (Fig. 1). Most catches are taken close to the bottom over depths of 60–200 m near the break-in-slope of the continental shelf, as well as at the edges of troughs in Queen Charlotte Sound (QCS) and Hecate Strait (HS). Adult bocaccio can be semipelagic and are found over a variety of bottom types, although harvesters suggest they favour proximity to high relief and rocky bottom. In British Columbia, bocaccio are caught by trawl and hook-and-line gear along with many other groundfish species, including Pacific ocean perch (*S. alutus*), yellowtail rockfish (*S. flavidus*), canary rockfish (*S. pinniger*), and lingcod (*Ophiodon elongatus*).

Indices from seven trawl surveys (Fig. 1) were used in our study. Four of the surveys, 1) the west coast of Vancouver Island groundfish (WCVI Gfish), 2) Queen Charlotte Sound groundfish (QCS Gfish), 3) Hecate Strait groundfish (HS Gfish), and 4) west coast of Haida Gwaii groundfish (WCHG Gfish) represent a set of nonoverlapping bottom trawl surveys that were started between 2003 and 2006 to collectively survey most of the B.C. coastal shelf between 50 and 500 m of bottom depth. The focus of these surveys was to provide relative indices of all groundfish species affected by the groundfish bottom trawl fishery in B.C. waters. For all four surveys, the Atlantic Western II groundfish bottom trawl was used and the surveys were conducted by the Canada Department of Fisheries and Oceans (DFO) staff on either the government research trawler (surveys 1 and 2) or chartered trawler (surveys 3 and 4).

Two of the surveys, the WCVI shrimp (survey 5) and QCS shrimp (survey 6) are conducted by DFO staff on board the same DFO research trawler (Boutillier et al., 1998). These surveys use a shrimp trawl and were designed to provide relative indices of shrimp abundance on two specific shrimp fishing grounds. For the seventh survey, the U.S. triennial survey a Nor'Eastern groundfish bottom trawl was used. This survey was designed to monitor groundfish abundance in U.S. waters, but in some years covered a small portion of southern B.C. waters. This survey stopped covering Canadian waters after 2001.

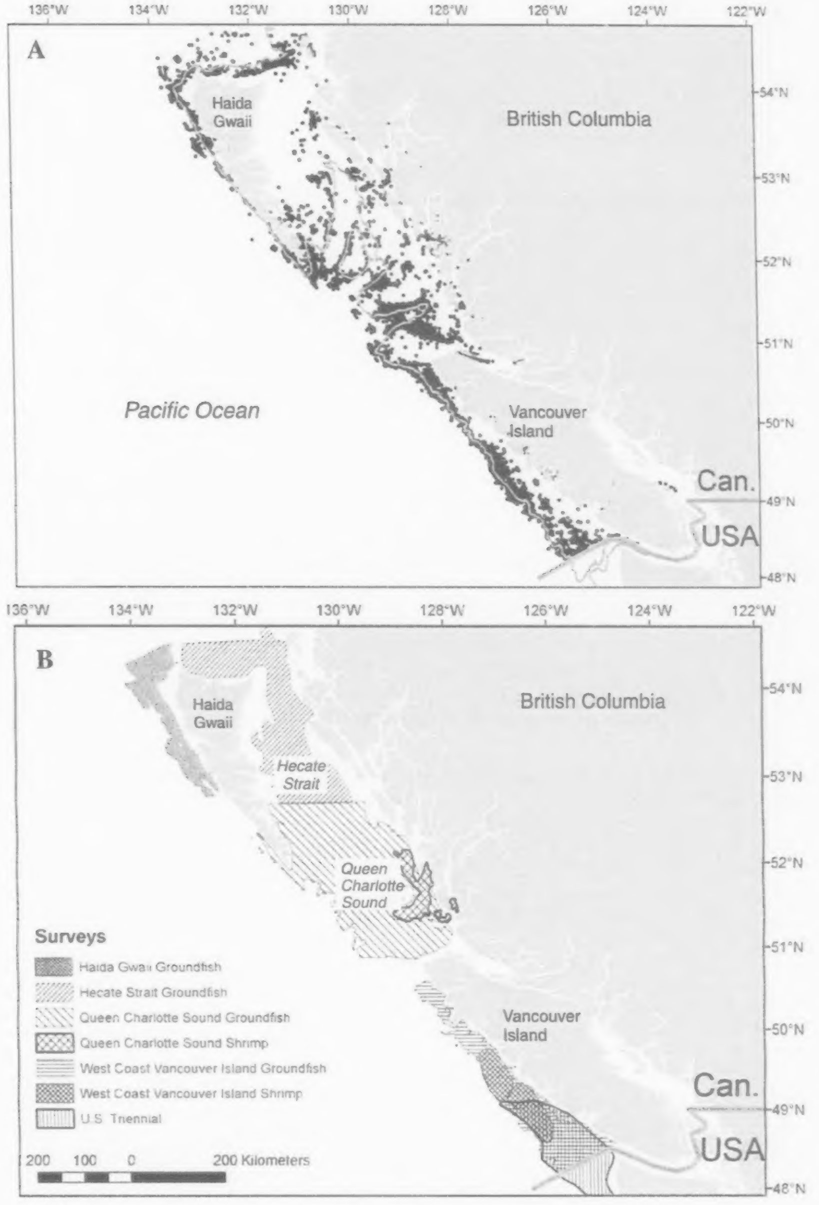
Methods

General model structure for trawl survey catchability (q_{gross})

See Table 1 for descriptions of all symbols used in this paper and Figure 2 for a schematic outline of the inputs, sub-models and outputs of the q prior model. We define catchability (q_{gross}) as the ratio of biomass of rockfish in a particular survey area to the population biomass of a given rockfish population that is on average vulnerable to trawl survey gear on account of gear selectivity (i.e., the fully vulnerable population biomass). q_{gross} is typically considered to be the long-term average value and is applied as a scalar to the fully vulnerable population biomass (B_y) modeled in a stock assessment model to predict the index of biomass obtained from a given trawl survey. The predicted swept-area biomass ($\hat{I}_y$) is obtained from the product of B_y and q_{gross}:

$$\hat{I}_y = q_{gross} \times B_y \quad (1)$$

For rockfish, it has been generally acknowledged that there are three main factors that may cause the value


136°W
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A
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Vancouver Island
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Hecate Strait
Queen Charlotte Sound
Surveys
Haida Gwaii Groundfish
Hecate Strait Groundfish
Queen Charlotte Sound Groundfish
Queen Charlotte Sound Shrimp
West Coast Vancouver Island Groundfish
West Coast Vancouver Island Shrimp
U.S. Triennial
200 100 0 200 Kilometers

Figure 1

(**A**) Locations where bocaccio (*Sebastes paucispinis*) were caught in commercial and research trawls, 2004–08. The 200-m depth contour is shown by a thin gray line. (**B**) Locations of trawl surveys in outside waters of British Columbia.

for q_{gross} to deviate from unity and may be conceived to act multiplicatively (Millar and Methot, 2002):

$$q_{gross} = q_{net} \times q_{trawlable} \times q_{available}, \qquad (2)$$

where q_{net} = the fraction of exploitable biomass that is within the path (i.e., between the trawl doors) of a given type of survey net and that is on average captured by the net;

Table 1

Definition of symbols for the indices, model parameters, and model variables used to determine trawl catchability for bocaccio (*Sebastes paucispinis*) off British Columbia.

Symbol	Description
Indices	
pop	entire fish population of interest that is potentially susceptible to capture by the survey gear of interest
n	trawl net type, e.g., in study 1=the groundfish AWII used in the Department of Fisheries and Ocean's groundfish trawl surveys, in study 2=the shrimp trawl, in study 3=the Nor' Eastern used in the U.S. triennial groundfish trawl survey
c	interviewed captain
s	survey
Model parameters	
q_{gross}	the parameter that scales the model-predicted population biomass to a trawl survey swept area biomass value
q_{net}	the parameter that reflects the fraction of exploitable biomass within the path (i.e., between the trawl doors) of a given type of survey net that is on average captured by the net
$q_{availability}$	the fraction of total exploitable population biomass indexed by a given survey (the proportion of the population biomass in the survey area)
$q_{trawlable}$	the parameter that accounts for the potential average difference in rockfish density between trawlable and untrawlable areas and the fraction of the surveyed area that is trawlable
S_s	the fraction of total population biomass present in the survey area
f_{Ts}	the fraction of the total survey area A that is trawlable.
α	the ratio of target rockfish density in untrawlable to trawlable habitat.
g_s	the bias correction factor to account for the difference in fish density between trawlable and untrawlable bottoms and the fraction of a survey area that is trawlable
$I_{T,s}$	swept area biomass obtained from trawl samples in the trawlable part of a survey area
n_{areas}	the number of surveyed areas in the range of an assessed fish population
a_1	estimate of the percent of rockfish that would be near-bottom (within 3–4 fm of the bottom, i.e., the kill zone) as the vessel passed overhead (Fig. 3)
a_2	proportion of off-bottom rockfish that "dive" into the kill zone (Fig. 3)
$a_{1.2.c}$	proportion of fish going into path of the net and doors from those in the water column that are in the horizontal path of the net and the doors (Fig. 3)
$a_{3,1.n}$	fraction of distance between the trawl doors that is in the path of the sweeps and bridles but more than 6 m inside of the door path (Fig. 3; Table 3)
$a_{3,2.n}$	fraction of distance between the trawl doors that is in the path of the sweeps and bridles but not more than 6 m inside of the door path, i.e., the fraction of fish in the "dead zone" inside which all fish are deflected out of the path of the net (Fig. 3, Table 3)
$a_{3.6.n,c,i}$	fraction of fish between the doors that end up in front of the net depending on whether the interviewed captain included the "dead zone" in assessing this fraction (i=1 means did not distinguish dead zone; i= 2 means did distinguish the dead zone) (Fig. 3)
$a_{4,n}$	relative proportion of fish remaining between the wingtips after excluding those in the deadzone (Fig. 3, Table 4)
$a_{5,n}$	relative proportion of fish in the herding zone after excluding those in the deadzone (Table 4)
$a_{6,n}$	proportion of the fish in front of the bridles and sweeps that would be herded into the path of the net
$a_{7,n,c}$	Proportion of fish that are captured of those that end up in front of the net
$a_{8,n}$	ratio of wingspread to doorspread used as a correction factor for q_{net} in instances where the swept area estimate has been computed based on the distance between the trawl net wingtips
$U_{n,c}$	Minimum threshold uncertainty factor (this factor could be made larger for net types with which a particular captain has had much less experience)
Model variables	
$\overline{I_{T,s}^{Su.A.}}$	average empirical swept area biomass estimate for the trawlable substrate in area s from the years in which survey took place in that area.
$n_{yr,s}$	number of years for which an estimate of swept-area biomass is available for a given survey in the reference year set
$lr_{s,i-j}$	predicted natural logarithm of the ratio of net i to net j catchability
$r\_ob_{s,i-j}$	observed ratio of density values from net i and net j for survey area s
SE_s	standard error in the mean of the natural logarithms of the swept-area biomass estimates in area s

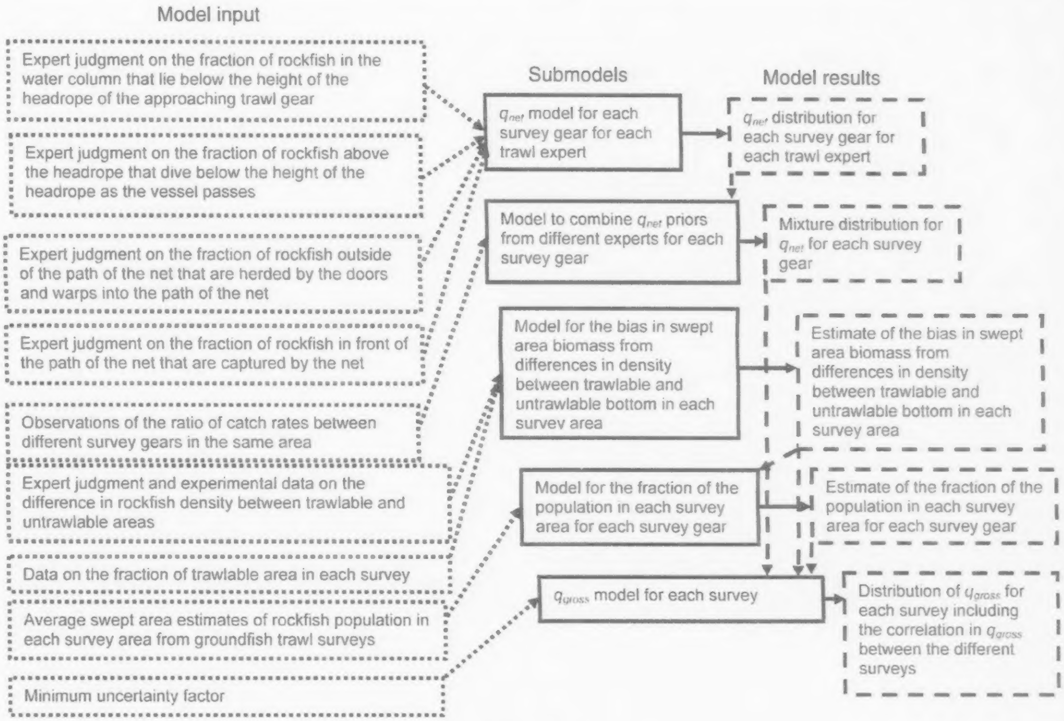
Model input
Expert judgment on the fraction of rockfish in the water column that lie below the height of the headrope of the approaching trawl gear
Expert judgment on the fraction of rockfish above the headrope that dive below the height of the headrope as the vessel passes
Expert judgment on the fraction of rockfish outside of the path of the net that are herded by the doors and warps into the path of the net
Expert judgment on the fraction of rockfish in front of the path of the net that are captured by the net
Observations of the ratio of catch rates between different survey gears in the same area
Expert judgment and experimental data on the difference in rockfish density between trawlable and untrawlable areas
Data on the fraction of trawlable area in each survey
Average swept area estimates of rockfish population in each survey area from groundfish trawl surveys
Minimum uncertainty factor
Submodels
q_{net} model for each survey gear for each trawl expert
Model to combine q_{net} priors from different experts for each survey gear
Model for the bias in swept area biomass from differences in density between trawlable and untrawlable bottom in each survey area
Model for the fraction of the population in each survey area for each survey gear
q_{gross} model for each survey
Model results
q_{net} distribution for each survey gear for each trawl expert
Mixture distribution for q_{net} for each survey gear
Estimate of the bias in swept area biomass from differences in density between trawlable and untrawlable bottom in each survey area
Estimate of the fraction of the population in each survey area for each survey gear
Distribution of q_{gross} for each survey including the correlation in q_{gross} between the different surveys

Figure 2

Outline of the structure of the trawl survey catchability model, showing the flow of information from model inputs to the model components (submodels) where the inputs are processed and integrated, to the final model results. See Table 1 for definitions of the variables.

$q_{available}$ = the proportion of B_y in the survey area; and

$q_{trawlable}$ = the average ratio of rockfish density between trawlable and untrawlable areas adjusted by the fraction of the seabed within the surveyed area that is trawlable.

We present conceptual models and equations for each of these components below.

Quantifying catchability with the trawl survey net (q_{net})

In most instances, results from experiments designed to estimate q_{net} for the survey gears and fish populations of interest are unavailable. Since the 1990s, some researchers have developed priors for q_{net} by integrating, within a Monte Carlo simulation model, expert judgment on the components of q_{net} and, in some instances, auxiliary data (Punt et al., 1993; McAllister and Ianelli, 1997; Boyer et al., 2001). Here we present a protocol for an approach that can be applied to estimates of biomass from trawl surveys when several experts provide key information, the population is surveyed by one or more types of trawl gears and, in one or more areas, records of catch rates from two or more types of trawl gears are available.

We first present a conceptual model for the components of q_{net}. It is assumed that a trawl net captures less than 100% of the fish that lie in its path, defined over the horizontal as the path between the trawl doors and over the vertical as the area from the surface to the bottom. Fish can escape for a variety of reasons including, but not limited to (Fig. 3), the following:

1 they are initially high up in the water column and do not "dive" to lie below the oncoming headrope of the trawl;
2 they are near bottom but are driven away horizontally by the influence of the warps near the doors as they spread outwards towards the doors;
3 they are initially in front of the paths of the sweeps and bridles but are not herded into the path of the net;
4 they escape over the headrope or under the footrope;

5 they are captured in the last few minutes of the tows and escape during retrieval (note that the DFO groundfish survey tows along the bottom last usually 19 minutes and in our application none of these fish were assumed to have escaped).

All of these potential sources of escape are factored into our catchability model.

We assumed that

1 q_{net} is constant among areas for the same type of trawl net;
2 q_{net} pertains to fishing during a bottom trawl survey, as opposed to commercial fishing. This assumption was emphasized to the trawl captains so that they would provide specifications based on standard trawl survey operations as opposed to commercial operating conditions; and
3 q_{net} does not vary with abundance.

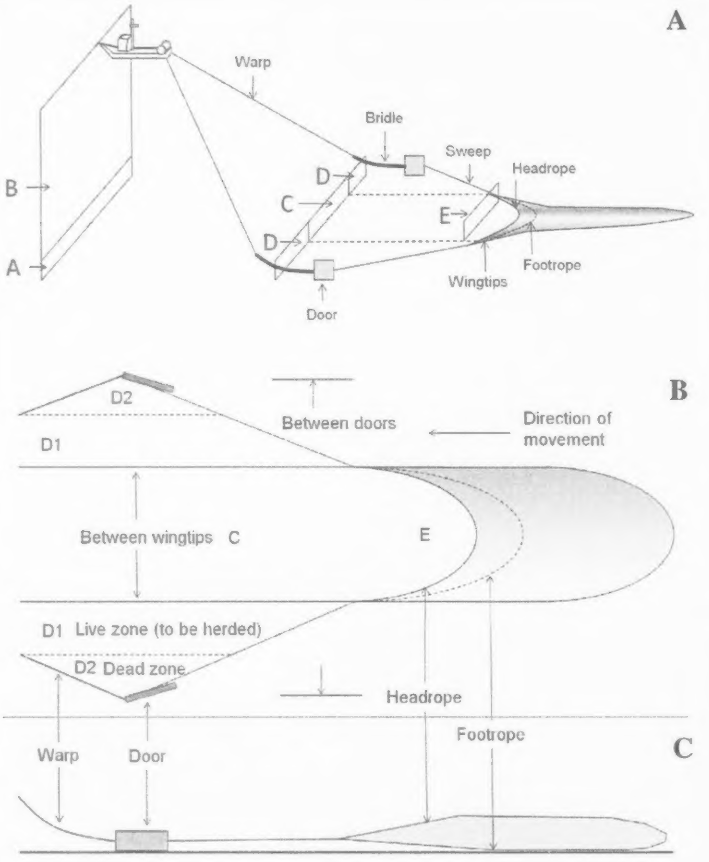

Figure 3

Diagram of fishing zones in the path of the bottom trawl. (**A**) Area A is the area below the boat between the doors and beneath the headrope. Area B is the area to the surface above area A. Area C is the area beneath the headrope to the footrope and between the net wingtips. Area D is the area beneath the headrope to the footrope and between the doors and the net wingtips. Area E is the area between the wingtips and beneath the headrope immediately in front of the trawl, i.e., the so called "kill zone," or capture zone. (**B**) Expanded top view and (**C**) side view showing the trawl warps, sweeps, and net configuration. D1, the "live zone" of the gear is the segment immediately outside of the wingtips in which rockfish are herded into the net path. D2, the "dead zone" of the gear, is the region just inside the trawl doors in which rockfish present escape from the pathway of the net. This conceptual scheme was used in interviews to enable trawl captains to express their views about the faction of rockfish in the water column that ended up in the trawl net.

$q_{trawlable}$-differences in fish density between untrawlable and trawlable areas

Trawl captains and groundfish researchers believe that the densities of rockfishes are higher over untrawlable bottom than over trawlable bottom. Note "untrawlable" is an operational distinction that reflects any type of bottom relief that trawl captains (research and commercial) judge as presenting too much risk for damage to the trawl gear. These opinions are based on the tendency for catch rates for virtually all rockfish species to be higher on, or nearer, rougher bottom, as well as the tendency for untrawlable bottom to be associated with a much stronger acoustic signal for rockfish, and on the basis of submersible studies, which indicate the tendency of rockfishes to be associated with rugged habitat (Krieger, 1993).

Estimates of biomass over swept areas are usually computed by assuming that the average catch rate of survey hauls in a given area (stratum) is a random sample of the entire survey area and, when multiplied by the total survey area, will provide the biomass index for the survey area. In this section, we present a bias correction factor to account for the average relative difference in fish density between trawlable and untrawlable areas in a surveyed area and the fraction of the surveyed area that is untrawlable.

It can be shown that the expected value for the survey biomass index when it is computed only from tows in trawlable habitat is

$$E(I_T)=\frac{q_{net}\,S\,B_{pop}}{\left(f_T+\alpha\left(1-f_T\right)\right)}, \tag{3}$$

where f_T = the fraction of the total survey area that is trawlable;
α = the ratio of fish density in untrawlable to trawlable habitat; and
S = the fraction of the total population biomass potentially susceptible to capture by survey gear (B_{pop}) and that is on average present in the surveyed area.

To briefly explore the implications of this equation let

$$g_s=f_{T,s}+\alpha(1-f_{T,s}), \tag{4}$$

where $f_{T,s}$ = the fraction of sea bottom in a surveyed area that is trawlable in survey area s; and
α = the ratio of target species density (t/km^2) in untrawlable to density in trawlable habitat.

Although α may vary with survey area, we typically do not have data that would allow us to estimate these separate factors and α therefore was assumed not to depend on s. In contrast, it is common to have data on the fraction of trawlable area within each survey area and therefore one can thus compute factor g for each survey area.

Should some experiment provide data on α, then the prior for α, $P(\alpha)$, could be statistically updated with the following equation:

$$P(\alpha\,|\,data)\propto P(\alpha)P(data\,|\,\alpha), \tag{5}$$

where $P(\alpha|data)$ = the posterior for α, given the data; and
$P(data|\alpha)$ = the probability of the data, given α.

Note that no such data were available for our case study application. $f_{T,s}$ can be treated as a beta random variable with binomial data on the number of trawlable sites for each area, or it can be fixed, if the number of trials in each area is very large.

$q_{availability}$-the fraction of total exploitable species abundance in each surveyed region

We developed a protocol to approximate the percentage of the coastwide target species exploitable biomass that is available to each of the surveys. This protocol computes and treats as a random variable the fraction of the total coastwide swept-area biomass in each survey area and accounts for potential differences between survey areas in the fraction of trawlable ground in each survey area. For this protocol, tow-by-tow data from the most extensive trawl survey (i.e., the "reference survey") were used. The protocol is illustrated with bocaccio as an example and includes the following assumptions:

1. The relative distribution of stock biomass among areas has been constant over a reference set of years and two or more groundfish trawl swept-area biomass estimates are available for all survey areas. For bocaccio this reference set covers the years from 2003 to 2007.
2. The proportion of untrawlable area to trawlable area within a surveyed region varies among regions and can be approximated from the observed frequencies of trawlable and untrawlable sites in the cumulative set of randomly allocated survey locations in each survey area. In fact, the locations found to be untrawlable are removed from the set of locations to be considered for research trawling in future years. However, in recent calculations we have found that the impact of this sequential removal of untrawlable locations on the estimated fraction of trawlable area is very small because the fraction of untrawlable areas is overall relatively small (less than about 20%).
3. The ratio of target species density in trawlable and untrawlable areas (α) is the same across areas and time.
4. The habitat for the target species is assumed to be the seabed area between a fixed depth range, e.g., 100–300 m in bottom depth for bocaccio.

Building on the above assumptions, we assume that the proportion of the coastwide target stock biomass available to each survey is the ratio of the swept-area biomass (adjusted for untrawlable area) estimated from trawl surveys during the reference-year period to coastwide stratified swept-area biomass of the target species (Table 2). For bocaccio, the coastwide swept-area biomass was the sum of the swept-area biomasses computed in each survey area from the DFO groundfish surveys plus a swept-area biomass estimate from the unsurveyed area not covered by the DFO groundfish surveys (Fig. 1B). This coastwide swept-area biomass includes regions over 100–300 m in bottom depth on the outer coast or in Hecate Strait (see, for example, in Fig. 1B the gap off the southwest coast of Haida Gwaii between the west coast of Haida Gwaii (WCHG) and QCS surveys). For the latter survey, a global estimate of species density was made across all trawl areas for the reference year period.

For surveys other than the reference survey (e.g., for bocaccio in the West coast of Vancouver Island (WCVI) shrimp survey, Queen Charlotte Sound (QCS) shrimp survey, and U.S. triennial surveys), the biomass of the target species present in the areas covered by the surveys was computed from densities observed in the ref-

Table 2

Estimates of bocaccio (*Sebastes paucispinis*) biomass with the swept-area method and based on Department of Fisheries and Oceans (DFO) groundfish surveys in each region in the years 2003–07. Percentage of coast-wide biomass refers to the fraction of coast-wide swept-area biomass (in regions 1–4, 8) that is on average found inside each region and is used in computing survey catchability. "SE ln(*bio*)" is the standard error for the mean of the natural logarithm of swept-area estimates of stock biomass in each region, with the mean determined from swept-area estimates in different years. "%Trawlable" is the estimate of the percentage of the region that was found to be trawlable based on random sampling of locations in each region for trawling and large sample sizes (>300 sites in each region). GFish=groundfish; WCVI=west coast of Vancouver Island; QCS=Queen Charlotte Sound; HS=Hecate Strait. WCHG=west coast of Haida Gwaii. The total is obtained only from the DFO groundfish survey because the other surveys are contained within it.

Survey number and region	Biomass (kg)[1]	Percentage of coast-wide biomass	Years of data	SE ln(bio)	% Trawable
1 WCVI Gfish	375,207	50	2004, 2006	0.0540	71.6
2 QCS Gfish	247,966	33	2003–05, 2007	0.2950	76.5
3 HS Gfish	35,340	5	2005, 2007	0.2670	78.3
4 WCHG Gfish	11,255	2	2006, 2007	0.0507	87.2
5 WCVI shrimp	20,787	3	2004, 2006	0.0262	100.0
6 QCS shrimp	27,767	4	2003–05	2.1010	100.0
7 U.S. triennial Gfish	180,599	24	2004, 2006	1.8590	82.0
8 Unsurveyed	76,664	10	2003–07	0.2020	0.0
Total	746,432				

[1] Computed from the product of the average density from the trawlable area and the total area of each survey area.

erence survey data set. Note that the regions covered by both shrimp surveys and the U.S. triennial survey lay within areas covered by the reference groundfish survey. For example, the biomass available in the WCVI shrimp trawl survey was based on the density observed in the tows conducted during the WCVI groundfish survey, within the area covered by the shrimp survey.

The fraction of total stock biomass, S_s in a given area s, can be obtained by

$$S_s = \frac{I_{T,s}\left(f_{T,s}+\alpha\left(1-f_{T,s}\right)\right)}{\sum_{j=1}^{n_{areas}} I_{T,j}\left(f_{T,j}+\alpha\left(1-f_{T,j}\right)\right)}, \tag{6}$$

where n_{areas} = number of regions for the reference survey plus 1 to account for the coastal habitat for the species that is outside of the surveyed area.

For the each region in the survey q prior model, $I_{T,s}$ can be considered a lognormal random variable:

$$I_{T,s} \sim \text{lognormal}\left(\ln\left(I_{T,s}^{med}\right), SE_s^2\right). \tag{7}$$

The cross-year median for the lognormal density function, $I_{T,s}^{med}$, in Equation 7 can be computed from the empirical mean swept-area biomass estimate ($\overline{I_{T,s}^{Sw.A.}}$) in each area s and the standard error (SE):

$$I_{T,s}^{med} = \overline{I_{T,s}^{Sw.A.}} * \exp(-SE_s^2/2), \tag{8a}$$

where

$$\overline{I_{T,s}^{Sw.A.}} = \frac{1}{n_{yr,s}}\sum_{y=1}^{n_{yr,s}} I_{T,s,y}^{Sw.A.}; \tag{8b}$$

$$SE_s^2 = \frac{1}{n_{yr,s}}\left(\frac{1}{n_{yr,s}-1}\right)\times \sum_{y=1}^{n_{yr,s}}\left(\ln\left(I_{T,s,y}^{Sw.A}\right)-\overline{\ln\left(I_{T,s}^{Sw.A}\right)}\right)^2; \text{ and} \tag{8c}$$

$$\overline{\ln\left(I_{T,s}^{Sw.A}\right)} = \frac{1}{n_{yr,s}}\sum_{y=1}^{n_{yr,s}}\ln\left(I_{T,s,y}^{Sw.A}\right), \tag{8d}$$

where $n_{yr,s}$ = number of years in which a swept area biomass estimate is available for a given survey in the reference year set.

The reference swept-area estimate for unsurveyed regions was obtained from stratified estimates of species density from trawled areas and the estimated habitat area outside of surveyed areas. Because the average catch per tow is based on tows over trawlable bottom, the swept-area estimate was adjusted to account for the estimate of the fraction of trawlable area in the survey area and the average relative difference in bocaccio density between trawlable and untrawlable bocaccio habitat (see Eq. 3).

Approach to acquiring information from trawl experts

Our approach relies on a large number of experts being interviewed to seek their judgments on the credibility of hypothesized values for factors affecting trawl-net catchability (q_{net}). A sufficiently large number of experts is required to characterize the range of differences in opinion among experts (e.g., Martin et al., 2005; Uusitalo et al., 2005). This can be achieved by continuing to sample until the distribution of inputs stabilizes, e.g., the means and standard deviations in inputs change by less than 10% for each new expert interviewed. In the interviews each trawl captain was asked to specify the most likely, minimum plausible, and maximum plausible average values for a set of key factors conjectured to determine q_{net} and these values were then used to formulate a triangular distribution for each factor for each survey net specific to each captain. The component factors of q_{net} formulated below represent "average" effects. Thus the minimum and maximum input values for each key factor do not reflect a predicted response for one case (i.e., from the population of all tows), but the minimum and maximum values for the average value across all tows combined. The pdfs formulated thus represent density functions of the mean value for a given factor, not the population of values from all conceivable tows.

The probabilistic modeling approach that was applied to synthesize the captains' inputs was similar to that taken by Uusitalo et al. (2005) and Martin et al. (2005) to formulate priors based on interviews with several different experts. For each net type, the resulting q_{net} was modeled as a mixture of the distributions resulting from the specifications from each of the interviewed captains.

Answers to our questions allowed us to simplify the process of catching a bocaccio to six steps based on four questions:

Step 1 Resolve the relative distribution in the water column (a_1). Question 1) *What is your best estimate (and minimum and maximum) of the percentage of target species that would be near-bottom (within 3–4 m) as the vessel passed overhead?*

Rockfish, particularly bocaccio, are presumed to occupy the water column from surface to bottom, but their density increases with depth. The factor, a_1, for the relative distribution of the target species in the water column (zone A, Fig. 3) defines the proportion of fish below headrope height, as the vessel passes over the fish. For this step, three assumptions are made:

1. fish below the headrope, as the vessel passes over them, continue to stay below the height of the headrope until they arrive at the mouth of the net;
2. fish outside the doors (horizontally), continue to stay outside the doors; and
3. a_1 is the same for all nets (this is reasonable because most of the nets have headline heights of around 3 m and only the U.S. triennial net is higher).

Step 2 Resolve the proportion of off-bottom target species that "dive" into the "kill zone" (i.e., the area immediately in front of the opening of the trawl net), (i.e., zone E, Fig. 3) (a_2). Question 2) *What percentage of those fish initially off-bottom would dive into the kill zone?*

The factor a_2 is the proportion of fish in zone B that would dive into the kill zone from those initially above the head rope of a given type of net (zone B, Fig. 3). For factor a_2, the following assumptions are made:

1. all fish below the headrope, stay below the headrope until at the mouth of the net;
2. fish dive in response to vessel noise and warps; and
3. dive rate is equal for all net-warp-vessel combinations.

Step 3 Resolve the proportion of fish which lie in the "dead" zone, i.e., the zone between the doors but external to the trawl warps.

The answers to questions 1 and 2 provided the percentage of fish that were initially in the path of the trawl doors that would lie in the capture zone as the doors approached (between the doors and below the headrope) (zones C–D, Fig. 3). The disposition of the fish horizontally would then be partially determined by whether they lay directly in the path of the net between or outside the wingtips but still within the door path. Fish in zone C were assumed to stay there as the net approached (zone E). Fish in zone D would have to be herded inwards to area C by the sweeps and bridles (Fig. 3).

Discussions with some captains indicated that for fish that lie within 6 m of doors inside the door path there is zero catchability. As the trawl warps approach the doors near the bottom, they spread out towards the doors, possibly scaring near-bottom fish out of the kill zone. Therefore, as the doors approach the fish, the fish are assumed to be distributed across the path of the doors in one of three sectors, in proportion to the linear dimensions of that sector (Fig. 3), namely:

1. in the path of the net (i.e., between wingtips, zone C, Fig. 3, Tables 3 and 4);
2. in the path of the sweep and bridles but more than 6 m (for survey nets used for bocaccio) inside of the door path (herding zone, D1, Fig. 3B) (factor $a_{3.1.n}$); and
3. in the path of sweep and bridles but within 6 m of the doors (dead zone, i.e., horizontal area in which all fish are expected to escape capture) (D2, Fig. 3B).

Step 4 Resolve arithmetic correction for the relative proportions of fish remaining in front of the net (between wingtips) or in front of sweeps and bridles (inside of the dead zone).

After allowing fish in the dead zone to escape, we estimated the proportions of remaining fish that either lie in front of the net (zone C, Fig. 3) (factor $a_{4.n}$) or the "herdable" section of the sweeps and bridles

Table 3

Relative distribution of fish in different sectors and parts of the kill zone of the gear as the gear approaches a stationary fish. The factors, proportion of the linear distance between the trawl doors that is within wingtips ($a_{3,1}$) and proportion in the dead zone ($a_{3,2}$) are used in the trawl survey catchability model. Distances are in meters. See Figure 3 for a schematic diagram of a trawl net.

Net type	Nominal door spread	Nominal wing spread	Nominal distance between doors, outside of wings	Dead zone in herding area	Effective herding zone	Proportion remaining in herding zone ($a_{3,2}$)	Proportion within wingtips ($a_{3,1}$)	Proportion removed by dead zone
AWII trawl (groundfish)	63.3	14.4	48.9	6.0	36.9	0.583	0.227	0.190
Nor'Eastern trawl (U.S. triennial)	58.9	13.4	45.5	6.0	33.5	0.569	0.228	0.204
Shrimp trawl	26.5	10.6	15.9	6.0	3.9	0.147	0.400	0.453

(zone D1, Fig. 3B, Tables 3, 4) (factor $a_{5,n}$) (see Eq. 10 for captains who explicitly accounted for the dead zone and Eq. 11 for those who did not).

Table 4

Relative proportions (P) of remaining fish in areas C and D1 (from columns 6 and 7 in Table 3, Fig. 3). Both of these factors (a_4 and a_5, respectively) are used in the trawl-survey catchability model.

Net	P between wingtips (a_4)	P in herding zone (a_5)
AWII trawl (groundfish)	0.281	0.719
Nor' Eastern trawl (U.S. triennial survey)	0.286	0.714
Shrimp trawl	0.731	0.269

Step 5 Determine the proportion of fish that will be herded from the path of the sweeps and bridles (zone D1) into the path of net (inside the wingtips) (zone C). Question 3) *What percentage of the fish in front of the bridles and sweeps would be herded into the path of the net?*

The factor a_6 concerns the remaining fish in sweeps and bridles path and for this step the following assumptions are made:

1 fish initially in front of the net, stay in front of the net; and
2 factor a_6 is the same for all nets.

Step 6 Determine the proportions of fish that are captured of those that end up in front of the net ($a_{7,n,c}$). Question 4) W*hat percentage of the fish that make it to area E will be captured and retained by the net?*

Finally, of the fish that have ended up in front of the net (zone E in front of footrope, Fig. 3), what percentage will be captured and retained in the net?

Steps in the algorithm to compute a prior probability density function for estimates of catchability

WinBUGS 1.4 (Lunn et al., 2000) was applied to synthesize the inputs from the trawl captains and other technical settings and to produce output density functions for the q_{gross} values for each of the surveys. The steps of the algorithm applied are provided below.

Step 1 Draw a value for the ratio of fish density in untrawlable areas to fish density in trawlable areas, α, from the density function for it (see Eq. 3 and below for specifications).

Step 2 To generate a value for the fraction of total population biomass vulnerable to survey gear in each area, S_s, draw a value for swept-area biomass in each of the eight coastal areas, using the lognormal density function and the empirical swept-area value as the median and the variance in the natural logarithm of the estimate (Eqs. 6–8, Table 2).

Step 3 For each captain, draw a value for the proportion of fish below the headrope (a_1) using the parameters of the triangular distribution provided by each captain.

Step 4 For each captain, draw a value for the proportion of fish above the headrope that stay above the headrope as the net approaches (a_2), using the parameters of the triangular distribution provided for each captain.

For each captain, compute the proportion of fish entering the path of the net and doors from those in the water column that are in the path of the net and the doors ($a_{1,2}$), such that

$$a_{1,2} = 1-(1-a_1)*a_2. \tag{9}$$

Step 5 For each captain, draw a value for the proportion of fish that will successfully be herded from the path of sweeps and bridles to the path of the net (one captain) or herded from the path of the doors to the path of the net (the other captains) ($a_{6,n}$).

Step 6 For each captain, compute the fraction of fish between the doors that end up in front of the net, given the proportion of doorspread that is between the wingtips ($a_{3,1,n}$) (step 3 of previous section) for the following sections of the gear—the dead zone ($a_{3,2,n}$), between the dead zone and the wingtips (of the area not in the dead zone) ($a_{4,n}$), and between the wingtips (of the area not in the dead zone) ($a_{5,n}$)—and the fraction of fish herded into the path of the net ($a_{6,n}$).

For the captains that conditioned herding of fish into the front of the net on those fish that swim in the zone between the doors and the wingtips, the following formula applies:

$$a_{3.6,n,1} = (1-a_{3,1,n}) \times a_{6,n} + a_{3,1,n}. \tag{10}$$

For the captain that conditioned herding of fish into the front of the net on those fish that swim in the area that does not include the dead zone, the following formula applies:

$$a_{3.6,n,2} = (1-a_{3,2,n}) \times (a_{4,n} \times a_{6,n} + a_{5,n}). \tag{11}$$

Step 7 For each net type (n) and captain (c), draw a value for the proportion of fish that are captured of those that end up in front of the net ($a_{7,n,c}$). To do this, use the parameters of the triangular distribution provided for each captain for each net type.

Step 8 Compute q_{net} for each net type (n) and captain (c):

$$q_{net,n,c} = a_{1.2,c} \times a_{3.6,n,c} \times a_{7,n,c}. \tag{12}$$

Step 9 Compute the q_{gross} for each survey (s) for each captain (c):

$$q_{gross,s,c} = q_{net,n,c} \times U_{n,c} \times S_S \,/\, (g_s \times a_{8,n}), \tag{13}$$

where $U_{n,c}$ = the uncertainty random variable for each net type and captain;
S_s = the random variable for the fraction of exploitable stock biomass in the region s;
g_s = the random variable accounting for trawlable area in region s; and
$a_{8,n}$ = the fixed correction factor applied where the wingtip distance had been applied to compute the swept-area biomass.

$U_{n,c}$, is applied to each $q_{net,n,c}$ to ensure that the density functions are not overly precise (i.e., it applies a multiplicative uncertainty factor).

Such factors have been applied in other situations where it is presumed that the distributions offered by experts are far too certain (e.g., Boyer et al., 2001). In our application, an uncertainty factor was drawn from a lognormal density function with a coefficient of variation (CV) of 0.5 and a median of 1 for each captain and net type. See the discussion for further justifications for including this factor and for the choice of the value for the CV.

Step 10 Give each captain's q_{gross} equal prior weight in the final q_{gross} distribution such that the chance of including a given captain's input has equal prior probability.

We applied a C-dimensional Dirichlet density function where C is the number of captains. This was applied as the multivariate prior pdf for the relative weight given to each captain's q_{gross} distribution for a given survey. All C input parameters for this density function were set to 0.5, which gives a relatively uninformative prior for the weight placed on each captain. In each Monte Carlo iteration, one of the C captain's q_{gross} values was randomly chosen for the q_{gross} random variable for each of the seven research surveys. Thus, without any Bayesian updating with new data, each captain's inputs are given equal weight in the output probability distribution q_{gross} for each regional survey.

Step 11 Use observations of the ratio of average catch rates from the different survey gears, e.g., shrimp trawl and groundfish trawl, from comparative gear experiments in specific locations (intended or unintended) to update the $q_{net,c}$ density functions for these survey nets (see Eqs. 14–15 below).

The ratios of observed average catch rates for the different survey nets will give more weight to captain inputs that are more consistent with the observed ratios for these two net types.

Step 12 Apply WinBUGS (or other Bayesian integration software) to produce two or more sets of Markov chain results for the q_{net} parameters for each net type and q_{gross} parameters for each survey; apply diagnostics to remove the burn-in and summarize the posterior results.

Step 13 Evaluate the posterior correlations between the q_{gross} parameters for the different surveys and identify a suitable multivariate density function to summarize the results.

Because the q_{gross} distributions for the different survey regions in our application were computed with identical input values for q_{net} across survey regions, the q_{gross} variables tended to be highly correlated across survey regions. There is the potential for multimodality in the marginal density functions for q_{gross} for the different survey areas and thus a mixture distribution may be appropriate. Should the results for each survey be unimodal, then a multivariate lognormal density function should be a good candidate.

Implementation of the method for bocaccio

In the q prior model for British Columbia bocaccio, we treated the factor α as a random variable, having a triangular prior distribution with a minimum of 1, maximum of 10, and mode at 3. f_T is provided by survey area (Table 2) and treated as known because the number of sites sampled per survey area was high in all areas (300–1000 depending on the survey area). Shelf regions without trawl surveys (unshaded regions in Fig. 1B) were excluded from the original set of groundfish surveys because the fraction of trawlable seabed was known to be very low. Thus, f_T in areas where there are no surveys is presumed to be 0%

The average and standard error (SE) in the average of the natural logarithm of the available estimates of annual swept-area biomass for each survey region (Table 2) were computed and applied in the q prior model to generate from a lognormal density function samples of potential stock biomass in each region and the potential fraction of total stock biomass in each region. Some of these standard errors were very large and created large uncertainty in the fraction of stock biomass for each of the regions. Note that in instances in which the SE is less than 0.15, we recommend that this value be set to 0.15, because, in general, the minimum CV in a swept-area biomass, accounting for all sources of error variability (i.e., SE divided by the mean) for relative stock size, should be no less than 0.15 (the CV of a lognormal distribution is $\sqrt{\exp(\sigma^2)-1}$, where σ is the SD in the natural logarithm of the random variable). The empirical values for SE may be low because of small sample sizes (e.g., n=2 years) and chance. We believe that because of the highly clumped spatial distribution of bocaccio, longer time series would yield higher values for SE than were obtained when the empirical values happened to be less than 0.15.

The U.S. triennial survey and the two shrimp surveys are contained within the WCVI and QCS groundfish surveys (Fig. 1B). These larger surveys that contain the smaller, more localized ones are called here "containing surveys." For the smaller or "contained" surveys, the random variable (RV) for $I_{T,s}$ was limited to the product of the fraction of area occupied by the contained survey and the RV for $I_{T,s}$ for the containing survey. This computation presumes that bocaccio density in the contained survey is no larger than that in the containing survey and limits the biomass for the contained survey to no more than that expected if the density was the same between the contained and containing survey.

In our application, we consulted with 12 commercial trawl captains—each with at least 10 years of experience in trawling for rockfish. All captains had experience (11–22 years) with types of trawls used in the DFO groundfish and U.S. triennial surveys, i.e., both groundfish and shrimp trawl nets, and with total groundfish landings ranging from 6800 to 275,000 t. Captains 1–4 were interviewed in groups of two and the remaining captains were interviewed separately. An attempt was made in each interview to provide the same explanation for the requested information, although the interview was conducted in an informal conversational manner. The format undoubtedly varied in subtle ways over the course of the 12 interviews. During our interviews with trawl captains, we characterized "typical survey fishing" as occurring on average at 150 m depth from June to July from 1 h after sunrise to 1 h before sunset. This fixed interval of time was necessary because trawl captains preferred to answer the questions while considering specific fishing conditions (i.e., time, depth, season, etc.)

For bocaccio, only one of the captains presumed that the a_6 proportion reflected the proportion of fish between the dead zone and the path of the net that are herded into the path of the net. The rest of the captains presumed that this proportion reflected the fraction of fish between the doors and the path of the net that are herded into the path of the net. The doorspread of the U.S. triennial survey Nor' Eastern trawl net was not measured. We assumed it had the same ratio of wingtip to doorspread as that of the Atlantic western (WII) trawl net used in the DFO groundfish survey.

For the q_{net} interview questions, each captain was asked for catch estimates for each of the three nets. The nets are towed at different speeds, have different vertical openings and, perhaps most importantly, the mouth opening of the shrimp trawl is not configured, so that the headrope overhangs the footrope (known as a "cape"). The net parameters are as follows:

1 DFO Atlantic Western trawl: towed at ~3 knots, and having a 3.7-m vertical opening;
2 U.S. Nor' Eastern trawl: towed at ~3 knots and having a 7.1-m vertical opening; and
2 DFO shrimp trawl: towed at ~2 knots and having a 2.7-m vertical opening.

Most groundfish trawls have a shorter headrope than footrope so that the headrope precedes the footrope through the water providing a "cape" or "hood." As a fish encounters the footrope, it cannot escape by swimming directly up. On the shrimp trawl, however, the headrope and footrope are virtually in line. Presumably, when the bocaccio detect the proximity of the mouth opening of the shrimp trawl, the net front is already effectively a 2.7-m vertical "wall" of footrope, disturbed sediment, and headrope. It is reasonable to assume that some bocaccio would escape vertically. When a bocaccio encounters the groundfish footrope, however, it is surrounded on four sides (wings, cape, and the bottom). We assumed that the relatively large bocaccio did not escape through the net and that the probability of retention was 1. The value for this factor, $a_{7,n}$, depends on the net ($a_{7,1}$ for the AWII trawl, $a_{7,2}$ for the triennial Nor'Eastern, $a_{7,3}$ for the DFO shrimp trawl). Our approach derives catchability based on doorspread, and therefore the U.S. triennial and the WCVI shrimp trawl estimates first had to be altered by the ratio of wingspread to doorspread ($a_{8,n}$).

Table 5

Biomass estimates of bocaccio (*Sebastes paucispinis*) based on survey tows using the shrimp trawl survey net and the Atlantic western (WII) groundfish trawl survey net, Estimates were based on survey positions shown in Figures 4 and 5. Results are shown for Queen Charlotte Sound (2003–07 for shrimp trawl and 2004–05 for AWII groundfish) and west coast of Vancouver Island (2004, 2006). The ratio of catch rates between these two survey gears was used to screen the plausibility of values for trawl-net catchability for these two nets that was determined from the interviews of the trawl captains.

	Shrimp trawl		AWII groundfish trawl	
Region	Number of tows	Biomass (kg)	Number of tows	Biomass (kg)
Queen Charlotte Sound	212	4993	52	39,746
West coast of Vancouver Island	141	5258	66	20,787

The shrimp and groundfish survey gears were applied in the same years in the survey area of the WCVI shrimp survey and the QCS shrimp survey. The observed mean ratio of bocaccio density between the trawl and shrimp survey nets for QCS for the years 2003, 2004, 2005, and 2007 was 8.76, with a SE in the natural logarithms of the estimates of 0.59 (Table 5, Fig. 4). The observed mean ratio for density estimates for the WCVI shrimp survey region between the groundfish and shrimp nets for the years 2004 and 2006 was 3.95, with a SE of 0.116 (Fig. 5). This latter SE was increased to 0.3 for the statistical estimation, because it was judged unlikely that the precision could be so high and there were only two years of survey data to provide this estimate. In each Monte Carlo iteration, the natural logarithms of the computed q_{net} values chosen for the shrimp and groundfish surveys were taken and the logarithm of the q_{net} for the shrimp survey was subtracted from the logarithm of the q_{net} for the groundfish survey. This difference was used as the expected log ratio for these survey catch rates for these two types of trawl nets. A lognormal density function was then applied to compute the probability of the observed ratio, given the model predicted ratio of q_{net} for these two nets:

$$lr_{s,i-j} = \log(q_{n=i,s}) - \log(q_{n=j,s}) \text{ and } i \neq j, \tag{14}$$

$$r\_ob_{s,i-j} \sim \log normal(lr_{s,i-j}, \sigma_{s,i-j}{}^2), \tag{15}$$

where the subscripts i and j denote the DFO groundfish survey and shrimp survey nets; respectively, and

$r\_ob_{s,i-j}$ = the observed ratio of density values from groundfish and shrimp nets for survey area s.

As indicated above, there are two observed ratios for bocaccio; one for the WCVI and one for QCS. For WCVI, $\sigma_{s,i-j}$ was 0.3, and for QCS, $\sigma_{s,i-j}$ was 0.59.

The WinBUGS results for bocaccio were numerically stable after

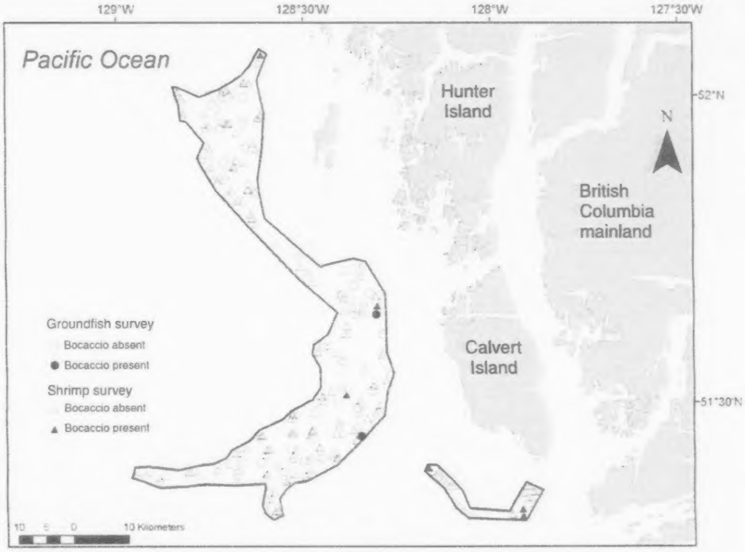

Figure 4

Mapped zones and trawl tow positions (symbols) of the Queen Charlotte Sound groundfish and shrimp trawl surveys where the two surveys overlapped. These two surveys provided an unintended reference source of the catch-rate ratio data for these two survey gears that were then used to update the groundfish-to-shrimp trawl-net catchability ratios for each of the experts. Polygons surrounding the overlapped survey areas were connected by hand to delimit the outer boundaries. Open and closed circles indicate the absence and presence, respectively, of bocaccio (*Sebastes paucispinis*) in the groundfish surveys. Open and closed triangles indicate the absence and presence, respectively, of bocaccio in the shrimp surveys.

rapid burn-in and rapid mixing. The Gelman-Rubin (Brooks and Gelman, 1998) statistic was applied to assess the burn-in period, which was judged to be about 500 iterations. A total of 40,000 iterations with two chains were judged to be sufficient to provide precise approximations of the target density function. Using the results after the burn-in, we found that the ratio of Monte Carlo error (analogous to standard error in the sampled posterior mean) to the posterior standard deviations (SDs) for all outputted variables was far less than the minimum standard of 5% (Best and Thomas, 2000).

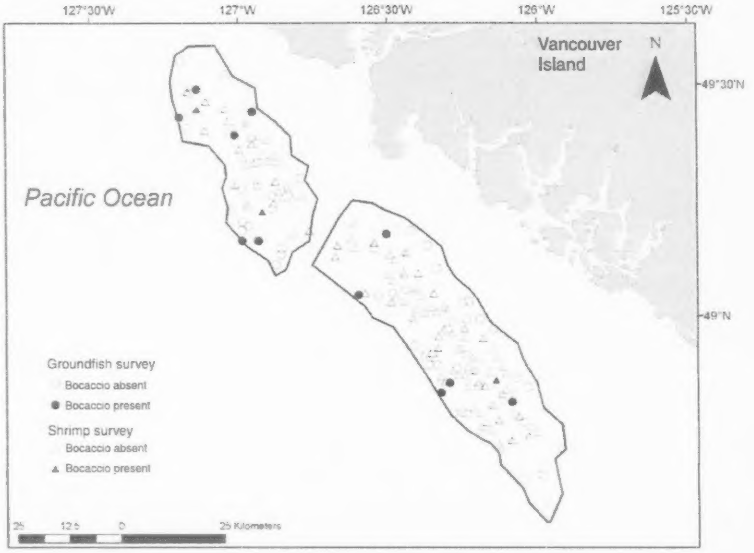

Figure 5

Mapped zones and trawl tow positions (symbols) of the west coast Vancouver Island groundfish and shrimp trawl surveys where the two surveys overlapped. These two surveys provided the catch-rate ratio data for these two survey gears that were then used to update the groundfish-to-shrimp trawl-net catchability ratios for each of the experts. Polygons surrounding the overlapped survey areas were connected by hand and delimit the outer boundaries. Open and closed circles indicate the absence and presence, respectively, of bocaccio (*Sebastes paucispinis*) in the groundfish surveys. Open and closed triangles indicate the absence and presence, respectively, of bocaccio in the shrimp surveys.

Results

We first considered the individual distributions computed from each captain's inputs for the catchability of each of the three net types (q_{net}). For each of the three net types, a wide range of plausible values for q_{net} were obtained from the 12 interviewed captains and there was considerable variability between the captains and some of the distributions were nonoverlapping (Fig. 6). The CVs in the q_{net} distributions by captain for each net varied from about 0.1 to 0.6, reflecting considerable variability in individual levels of uncertainty in the q_{net} inputs.

The q_{gross} values obtained for each captain and for each net type with no updating and no uncertainty factor showed considerably wider distributions and more overlap in all cases between the captains than the q_{net} distributions for each captain (Figs. 6 and 7). The q_{gross} distributions for the different surveys showed varying amounts of overlap between the captains with the WCVI shrimp survey showing the least amount of overlap and the U.S. triennial survey showing the most overlap because of very low precision in q_{gross} among captains. The low precision was primarily due to the high uncertainty in the fraction of stock biomass in the U.S. triennial survey area (Table 2). The CVs in the q_{gross} distributions by captain ranged from about 0.3 to 0.7 for the DFO groundfish surveys and the WCVI shrimp survey (Fig. 7). However, the QCS shrimp survey showed high CVs of about 1.5–1.8 because of the added uncertainty in accounting for the fraction of the stock in each survey area and the ratio of bocaccio density in untrawlable and trawlable areas. The q_{gross} distributions for the shrimp trawl surveys (e.g., for WCVI) were centered considerably lower than those provided for the groundfish surveys partly because of low values for q_{net} and because a small fraction of the stock falling in these areas. Also for the shrimp trawl survey areas, the fraction trawlable was 100%, whereas the groundfish trawl survey areas this was closer to 70–80% (Table 2).

We next consider different approaches to combining the q_{net} distributions from the different experts into a single q_{net} distribution for each net type. When equal weighting was applied to the inputs from the different captains without Bayesian updating and without the uncertainty factor, the q_{net} distributions for each net were multimodal (Fig. 8). Under these same conditions, the combined distributions for q_{gross} for each net showed varying amounts of departure from unimodality; the q_{gross} distribution for the WCVI shrimp survey showed the most pronounced bimodality (Fig. 9). When the uncertainty factor was applied without Bayesian updating, the q_{net} distributions showed less pronounced multimodality (Fig. 8); multimodality was no longer seen in any of the q_{gross} distributions and the distributions became slightly wider (Fig. 9, Table 6).

We compared the ratios in values of q_{net} for the groundfish survey to q_{net} for the shrimp survey (provided by the captains) with the observed ratios in values of q_{net} for the groundfish survey to q_{net} for the shrimp survey in the WCVI and QCS surveys

(Fig. 10). s/b10Although the observed ratios for WCVI and QCS were about 4 and 9, the ratios obtained from the captains' inputs ranged from about 1 to 32 (Table 7). The CVs in the expertly determined ratios ranged from about 0.1 to 0.5, conveying a range of degrees of uncertainty between captains (Table 7). Where the captains' ratios deviated most from the observed ratios and had the smallest CVs, the posterior probability for the captain was effectively zero or very low. This situation occurred for six of the captains (Table 7). In contrast, ratios that deviated considerably from the observed ones but had high uncertainty, e.g., for a captain whose mean ratio was 0.7 and CV was 0.4, still retained some posterior weight whereas captains with mean ratios of 1.3 and 1.5 but much smaller CVs had effectively zero posterior weight. The posteriors for the six captains that retained most of the weight ranged from about 0.06 to 0.38. These posteriors showed, if anything, a negative correlation (about −0.10 to −0.30) with the three measures of trawling experience (years of experience, and tons of groundfish and bocaccio landed) (Table 8). Therefore, although an expert's amount of experience may be a reliable indicator of his or her technical proficiency (i.e., the estimates of total groundfish landings and total bocaccio catch are strongly positively correlated with years of experience), experience does not indicate the reliability of the information that he or she may provide.

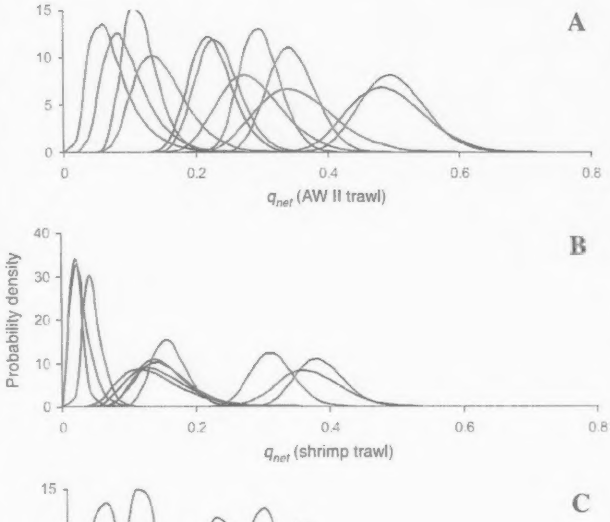

Figure 6

Probability density functions for trawl survey net catchability (q_{net}) for each captain for the (**A**) Atlantic western (AWII), (**B**) shrimp, and (**C**) Nor'Eastern trawl nets, based on inputs provided for each captain without any Bayesian updating and without the uncertainty factor applied.

When Bayesian updating was applied without the uncertainty factor, most of the weight shifted from three modes for q_{net} to predominantly two modes for each net type (Fig. 8). For example, the third mode over the highest values in the shrimp q_{net} posterior was eliminated. The central tendencies for the shrimp q_{net} and q_{gross} values decreased by about 40%, whereas that for the DFO AWII nets increased by no more than about 5% with the Bayesian update. Under these same conditions, precision in the q_{gross} distribution for each survey increased only for the shrimp surveys (Table 6). Bimodality was no longer present in the q_{gross} distributions (Fig. 9). In contrast to the instance with no uncertainty factor and no Bayesian updating, when Bayesian updating and the uncertainty factor were applied, the q_{net} distributions by captain all overlapped for each of the three nets (Fig. 10). The mean value for q_{net} for the shrimp trawl was lower and more uncertain than for the two groundfish nets (Fig. 8). None of the q_{net} and q_{gross} composite distributions showed bimodality and results were not quite as precise as with the analogous case without the uncertainty factor (Figs. 8 and 9, Table 6). The CVs in the groundfish survey q_{gross} values ranged from about 0.77 to 0.83; and 95% probability intervals (PIs) ranged between 22- and 25-fold between the bounds (Table 9). The CVs for the shrimp survey q_{gross} values were considerably higher at about 1.5 and 2.7 (95% PIs of about 84- and 3100-fold). This high uncertainty was largely due to large differences between the inputs provided by captains but also due to higher uncertainty in the fraction of stock in these surveys (Table 2). The U.S. triennial survey q_{gross} had a high CV (1.7) and an 800-fold 95% probability interval (PI). This high uncertainty is also due mainly to the high uncertainty in the fraction of the stock in this survey (Table 2).

One key factor is the ratio of fish density in untrawlable areas to that in trawlable areas, α. When this factor was set to 1 and the Bayesian update and uncertainty factor were applied, the central tendencies of the posterior distributions for all of the surveys approximately doubled, indicating that the effect of this parameter is to decrease q_{gross} for all surveys and to lead to increased population biomass estimates (Table 6). Doubling the mode and maximum value for α from 3 and 10 to 6 and 20 caused the mean for q_{gross} to decrease

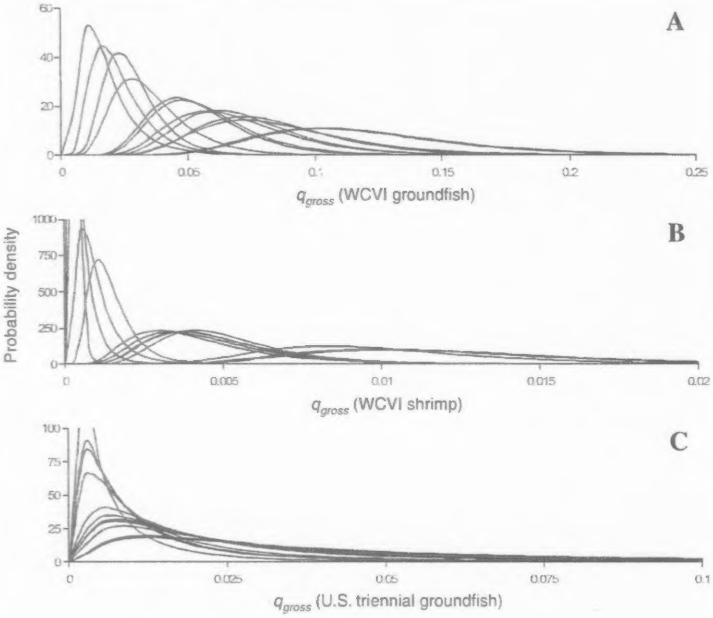

Figure 7

Probability density functions for trawl survey catchability (q_{gross}) obtained for each captain for the (**A**) west coast Vancouver Island (WCVI) groundfish, (**B**) WCVI shrimp, and (**C**) U.S. triennial groundfish surveys, based on inputs provided for each captain without any Bayesian updating and without the uncertainty factor applied.

to between 63% and 81% of the reference case values. The CVs for q_{gross} for the different surveys decreased slightly when α was set to 1 and increased slightly when its input distribution mode and maximum were doubled (Table 6).

The q_{gross} values for the different surveys showed varying amounts of positive correlation, which resulted from the use of the same or very similar nets in all of these surveys and the captains prescribing highly correlated prior inputs as in the case of the AWII and Nor'Eastern nets (Table 10, Fig. 8 shows a high degree of similarity in the q_{net} outputs for these two nets). The q_{gross} values for the DFO groundfish survey nets showed the highest correlations with values up to about 0.96. The q_{gross} for the U.S. triennial survey showed the lowest correlations with the other nets because of the high amount of uncertainty in the fraction of the population in this survey (correlations between 0.14 and 0.35). The QCS shrimp q_{gross} also showed low correlations with the other surveys also because of the high uncertainty in the fraction of the population in this survey area.

In our application, density functions for q_{gross} were unimodal and in all instances positively skewed. Thus, a multivariate lognormal density function was formulated to summarize the joint prior density function for q_{gross} for the six survey time series used in the stock assessment. This multivariate density function was formulated using the posterior median and covariance outputs from the WinBUGS (Tables 10 and 11). The prior results for q_{gross} for six of the surveys were compared with posterior results for q_{gross} from a stock assessment of Bristish Columbia bocaccio for which a noninformative prior for q_{gross} was used (Table 11). All posterior medians for q_{gross} obtained from the stock assessment with noninformative priors for q_{gross} (Table 11) were inside of the 95% PIs for the informative q_{gross} prior (Table 11). However, in most instances the posterior medians were larger than the prior medians, indicating that the stock assessment data tend to produce stock biomass values lower than those indicated by the q_{gross} density function obtained in this study.

Some key stock assessment quantities are also shown that were obtained with a noninformative prior and the informative q_{gross} prior (Table 12). The posterior mean values for stock biomass at maximum sustainable yield, stock biomass in 2008, and replacement yield changed slightly with the use of the informative q_{gross} prior. In contrast, the posterior CVs for the current stock biomass and replacement yield decreased substantially with the use of the informative prior for q_{gross}.

Discussion and conclusions

We provide an approach to formulating a Bayesian prior for trawl survey catchability for rockfish that can integrate subjective judgment from several experts on factors affecting net catchability with data obtained from field experiments and trawl research surveys. The approach is useful for situations where a stock assessment model is to be fitted to one or more survey indices and although directed at rockfish surveys, it could be extended to other groundfish species. For this approach, data are used from a series of related trawl surveys covering most of the British Columbia continental shelf, all based on the same trawl gear, to provide estimates of the fraction of the population in each survey area. Bias correction factors are formulated and can be updated with experimental data that allow us to evaluate hypothesized average differences in target fish species density between trawlable and untrawlable areas and the fraction of area in the survey that is treated as untrawlable. The current approach presumes that experts all have experience with all of the types of nets that are used in the surveys or with nets that are very similar. The approach updates each captain's inputs on the basis of the consistency with observations from experiments where the ratios of catch rates between different types of survey nets were evaluated. This updating process reduced the degree of uncertainty in the prior by considerably modifying the posterior distributions, particularly for the most poorly understood gear—the shrimp trawl.

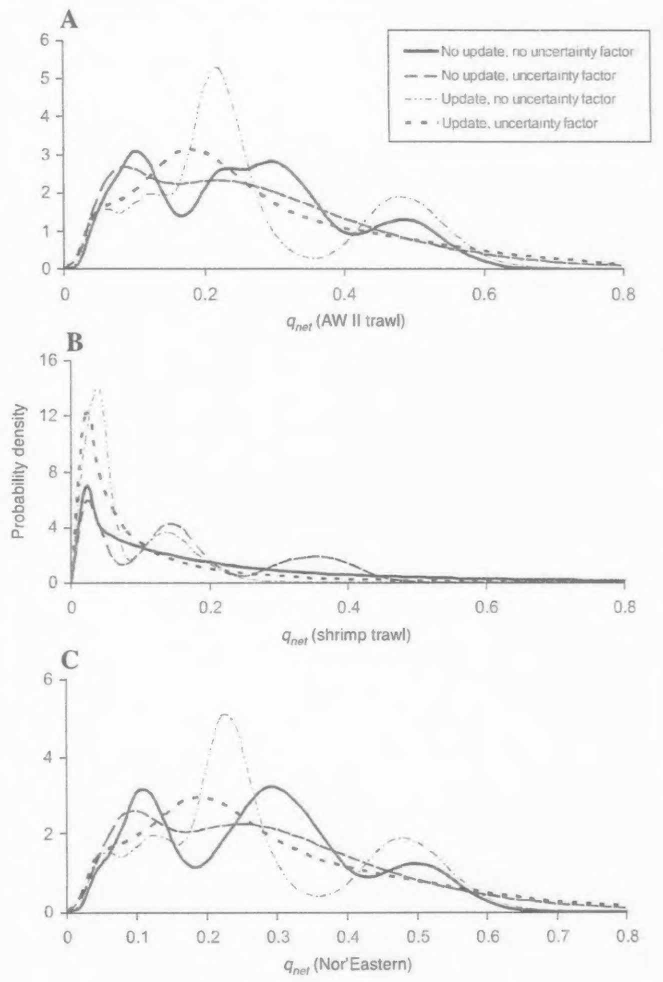

Figure 8

Probability density functions for trawl survey net catchability (q_{net}) for the (**A**) Atlantic western (AWII), (**B**) shrimp, and (**C**) Nor'Eastern trawl nets, based on inputs provided for each captain with and without any Bayesian updating, and with and without the uncertainty factor applied.

A few different procedures were applied to counteract the adverse effects on stock assessment results that may result from the tendency of individual experts to provide distributions that are too certain. One procedure was to apply an uncertainty factor (Boyer et al., 2001); this is discussed further below. The second was to apply a mixture distribution approach to incorporate judgment from different experts. However, this procedure may cause the resulting posterior distributions to be multimodal—a feature that may arise when the narrow distributions offered by the various experts fall into different modes. Such a result is less likely when there is a large number of contributing experts.

Attempts to directly estimate catchability with trawl nets (q_{net}) have met with limited success, particularly for rockfish. The principal difficulty lies in measuring the abundance of fish that is positioned in front of the net. Krieger and Sigler (1996) attempted to estimate catchability of Pacific ocean perch (*S. alutus*) for a bottom trawl on the basis of observations from a submersible vessel. They reported estimates for q_{net} of 0.97–1.27 for trawl catchability based on wingtip spread. Using the AWII to calculate an approximate ratio of doorspread to wingspread of about 4.4 (AWII, Table 3), they determined a doorspread catchability of 0.22–0.29 for Pacific ocean perch. Korotkov[1] used an underwater camera-mounted sled towed in front of the trawl to provide a ground-truth of actual fish density. He estimated a doorspread catchability of 0.1–0.4 for unspecified species of groundfish. Our estimates of q_{net} for bocaccio for three different trawl net types ranging from about 0.1 to 0.3 are similar to his estimates. Scientists at the Alaska Fisheries Science Center (NMFS) have spent many years attempting to estimate catchability of the trawl used in their west coast groundfish surveys. Their most successful work was with flatfish for which they observed maximum door-spread catchability for large arrowtooth flounder (*Atheresthes stomias*) of 0.47 (Somerton et al., 2007). The catchability for a flatfish such as arrowtooth flounder could be expected to be higher than that for rockfishes because bottom trawl nets are generally designed to capture flatfishes, which tend to stay very close to the bottom as opposed to many rockfishes, such as bocaccio, which tend to distribute themselves higher in the water column.

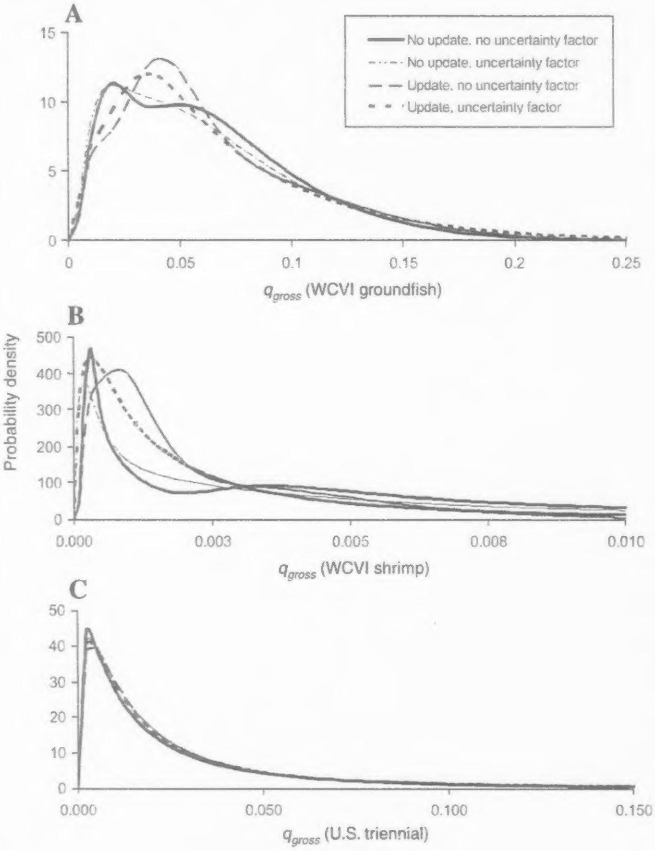

Figure 9

Probability density functions for trawl survey catchability (q_{gross}) for the (**A**) west coast Vancouver Island (WCVI) groundfish, (**B**) WCVI shrimp, and (**C**) U.S. triennial groundfish surveys, based on inputs provided for each captain with and without any Bayesian updating, and with and without the uncertainty factor applied.

Previous efforts at indirectly forming a prior for q_{gross} involved seeking expert judgment and, in some instances, adding auxiliary data to the components of q_{gross}, and then integrating these components within a Monte Carlo framework to formulate a pdf for q_{gross} (McAllister and Ianelli, 1997; Boyer et al., 2001). Different approaches were used to elicit information from experts. In some instances, the experts were interviewed separately to gain information on key factors determining q_{gross} (e.g., Punt et al. 1993, McAllister and Ianelli, 1997; Mosqueira, 2005). Another approach was to put several experts in the same room so that they could form a consensus on these factors (Boyer et al., 2001). An important limitation to these approaches has been that the posterior distributions often tend to be very narrow as a result that too few experts were consulted or that divergent opinions were forced into a consensus.

That experts often hold divergent views while each being certain about his or her knowledge has long been recognized as a problem when forming priors based on expert input. In the last decade, a number of analysts have suggested that it is important to retain this diversity as an output of the analysis and that it is unwise to eliminate the diversity by averaging across experts (Burgman et al., 1993; Chrome et al., 1996; Uusitalo et al., 2005). Some researchers have advocated assigning weights to experts according to their level of expertise (Burgman et al., 1993); others have assigned equal weighting to expert input, providing that all of these experts initially qualify to provide expert judgment (Martin et al., 2005; Uusitalo et al., 2005). It may not be desirable to assign different weights when the number of available experts is relatively few, because it is possible that a single expert may end up with all of the weight, thus defeating the purpose of the exercise.

We recommend applying an uncertainty factor to the for q_{net} variable obtained from each expert's inputs to

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[1] Korotkov, V.K. 1984. Fish behaviour in a catching zone and influence of bottom trawl rig elements on selectivity. Int. Council. Explor. Sea, Council Meeting 1984. B:15.

Table 6

Posterior means and coefficients of variation (CV) in the natural logarithm for bulk catchability (q_{gross}) under four different runs of the trawl survey catchability model with and without the Bayesian update and with and without the uncertainty factor applied. The values in the first column give the prior mean and CV for q_{gross} that could be used in a stock assessment. WCVI =west coast of Vancouver Island; QCS=Queen Charlotte Sound; HS=Hecate Strait. WCHG=west coast of Haida Gwaii.

Survey number and region	Bayesian update, uncertainty factor		Bayesian update, no uncertainty factor		No Bayesian update, uncertainty factor		No Bayesian update, no uncertainty factor		Bayesian update, uncertainty factor, same density in trawable and untrawable areas		Bayesian update, uncertainty factor, very high densities in untrawable areas	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
1 WCVI groundfish	0.070	0.77	0.067	0.67	0.068	0.76	0.065	0.66	0.145	0.68	0.046	0.85
2 QCS groundfish	0.046	0.80	0.044	0.71	0.044	0.79	0.042	0.70	0.094	0.71	0.030	0.89
3 HS groundfish	0.0067	0.83	0.0064	0.74	0.0064	0.82	0.0061	0.73	0.0137	0.75	0.0043	0.91
4 WCHG groundfish	0.0021	0.79	0.0020	0.69	0.0021	0.78	0.0020	0.68	0.0044	0.70	0.0014	0.87
5 WCVI shrimp	0.0030	1.46	0.0022	0.81	0.0072	1.63	0.0052	0.94	0.0062	1.36	0.0019	1.51
6 QCS shrimp	0.00036	2.74	0.00026	1.89	0.00086	2.92	0.00063	2.05	0.00054	2.52	0.00029	3.01
7 U.S. triennial groundfish	0.047	1.73	0.045	1.62	0.047	1.70	0.045	1.61	0.069	1.50	0.037	1.87

Table 7

The posterior mean ratio and posterior coefficient of variation (CV) for the ratios for trawl-net catchability (q_{net}) for the groundfish and shrimp trawl nets obtained from inputs provided by each of the captains. The posterior probability assigned to each captain's inputs is given in the last column.

Captain	Mean ratio	Mean CV	Posterior probability assigned to each captain's inputs
1	2.30	0.52	0.110
2	9.18	0.45	0.165
3	0.96	0.15	0.000
4	1.30	0.10	0.000
5	0.70	0.38	0.007
6	3.02	0.19	0.277
7	0.95	0.10	0.000
8	0.77	0.25	0.000
9	1.91	0.25	0.060
10	1.47	0.15	0.000
11	31.86	0.11	0.000
12	5.26	0.26	0.380

counteract the problem of experts being overly certain (Chrome et al., 1996; Martin et al., 2005; Uusitalo et al., 2005). The use of highly precise prior distributions for q has at least two adverse consequences for fish stock assessment. First, when a highly precise prior for q is applied (e.g., CV<0.4), the estimates of quantities of interest (e.g., virgin biomass, B_0) can be highly precise and exclude values consistent with stock assessment data (Boyer et al., 2001). Second, simulation evaluations have shown that when highly precise priors for q (e.g., with prior CV<0.5) that are centered over values as little as 50% higher or lower than the actual value, it takes many more years for stock assessment data to update precise priors than less precise priors centered over the same incorrect values (McAllister and Kirkwood, 1998). Application of a multiplicative uncertainty factor with a median of 1 and a CV of no less than about 0.5 maintains

Table 8

The correlation between measures of expertise and the posterior placed on each trawl captain's input. These correlations are presented to evaluate the presumption that the reliability of a trawl captain's judgment on trawl-net catchability increases with experience (i.e., the posterior probability on the captain should be positively correlated with years of experience). See *Results* section for further details.

	Years of experience	Total landings (t)	Total bocaccio catch (t)	Posterior probability obtained on a captain
Years of experience	1			
Total landings (t)	0.66	1		
Total bocaccio catch (t)	0.70	0.85	1	
Posterior probability obtained on a captain	−0.09	−0.29	−0.24	1

the central tendency of the experts' distributions and gives a prior CV in q_{net} for each expert that is no less than 0.5. Simulation evaluation has shown that prior CVs for $q \geq 0.5$ enable stock assessment data to override a biased prior for q within relatively few (e.g., 5–10) years (McAllister and Kirkwood, 1998). The choice of a CV of 0.5 is somewhat arbitrary but in our view necessary.

A hierarchical meta-analysis of stock assessment data from different populations of the same species group was applied to quantify the cross-stock central tendency and variability in q_{gross} for rockfish in the U.S. triennial survey (Millar and Methot, 2002). This approach has the advantage of avoiding expert judgment altogether and is tractable providing there is uniformity in the survey gear used in the different surveys. However, differences in behavioral responses to trawl gear among species could limit the validity of the assumption of exchangeability, which must be made in hierarchical modeling, and thus limit the applicability of the results as a prior distribution to an unsampled population. The log-transformed mode in the posterior pdf of "bulk" catchability equated to about 1.27 between the wingtips. The ratio of doorspread to wingspread ratio for this survey is not available but is probably similar to the approximately 4.4:1 ratio of the AWII configuration used in the DFO groundfish surveys and translates to a doorspread catchability estimate of about 0.29.

The priors provided in this study have higher CVs (0.8–2.7) than previous priors on survey q obtained from different experts (ranging from about 0.4–0.7, e.g., Punt et al. 1993; Boyer et al., 2001). This difference is partly due to the high uncertainty in the fraction of the population falling within each survey area which did not apply to the other studies because

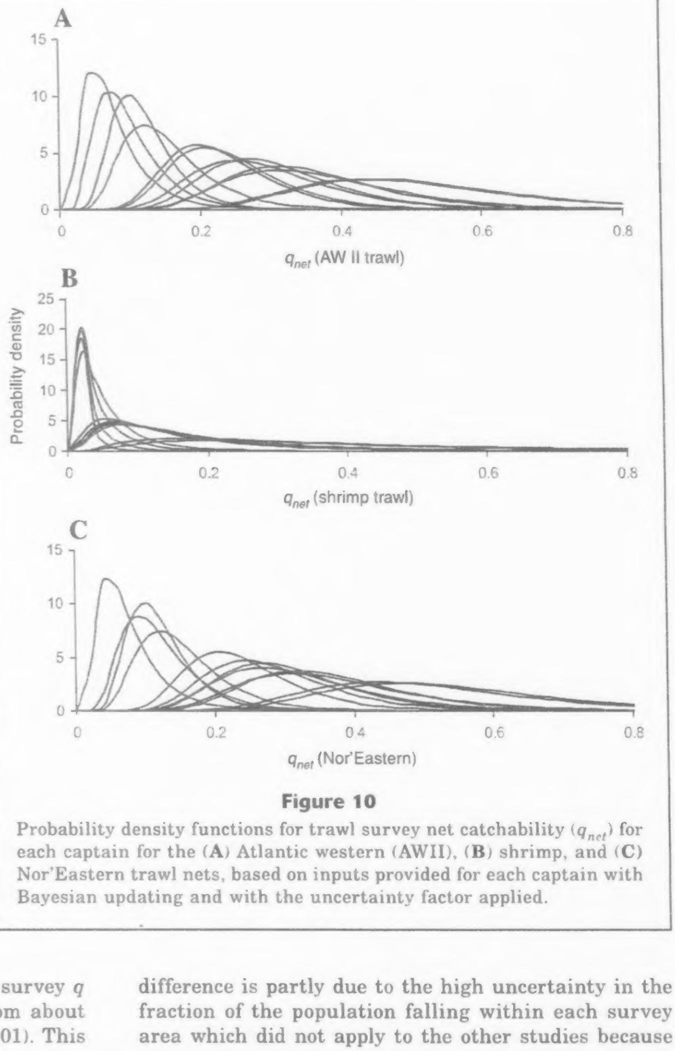

Figure 10

Probability density functions for trawl survey net catchability (q_{net}) for each captain for the (**A**) Atlantic western (AWII), (**B**) shrimp, and (**C**) Nor'Eastern trawl nets, based on inputs provided for each captain with Bayesian updating and with the uncertainty factor applied.

Table 9

Output statistics for q_{gross} for the run with the Bayesian update and with the uncertainty factor applied. Posterior means (mean), standard deviations (SD), and coefficients of variation (CV) are given. The last three columns show the 2.5th, 50th, and 97.5th percentiles. WCV=west coast of Vancouver Island; QCS=Queen Charlotte Sound; HS=Hecate Strait. WCHG =west coast of Haida Gwaii.

	Mean	SD	CV	2.5th	50th	97.5th
1 WCVI groundfish	0.070	0.054	0.77	0.010	0.055	0.212
2 QCS groundfish	0.046	0.037	0.80	0.006	0.036	0.143
3 HS groundfish	0.0067	0.0055	0.83	0.0008	0.0051	0.0215
4 WCHG groundfish	0.0021	0.0017	0.79	0.0003	0.0017	0.0067
5 WCVI shrimp	0.0030	0.0044	1.46	0.0002	0.0016	0.0143
6 QCS shrimp	0.00036	0.00098	2.74	0.0000008	0.0000730	0.00263
7 U.S. triennial groundfish	0.047	0.08225	1.73	0.0004	0.0161	0.287

Table 10

Posterior correlation matrix for the natural logarithm of the q_{gross} values for the seven surveys off British Columbia, during bocaccio (*Sebastes paucispinis*) were captured. The index number in the first column and first row indicates the survey for which the correlations apply. See Table 9 for a key to the survey indices.

	1	2	3	4	5	6	7
1	1.000						
2	0.912	1.000					
3	0.928	0.879	1.000				
4	0.963	0.912	0.929	1.000			
5	0.601	0.568	0.581	0.604	1.000		
6	0.312	0.311	0.305	0.315	0.526	1.000	
7	0.346	0.323	0.331	0.343	0.259	0.140	1.000

Table 11

Comparison of prior and posterior medians and standard deviations in the natural log of q_{gross} SD(ln$q$) before and after a stock assessment with noninformative priors for q_{gross}. See Tables 6 and 9 for the prior 95% probability intervals for q_{gross}. NA means not available. WCVI=west coast of Vancouver Island; QCS=Queen Charlotte Sound; HS=Hecate Strait. WCHG=west coast of Haida Gwaii.

	Prior for q_{gross}		Posterior for q_{gross}	
	Uncertainty factor, Bayesian update		After fitting assessment model to data with the noninformative survey q prior	
	median q	SD(lnq)	median q	SD(lnq)
1 WCVI groundfish	0.0534	0.78	0.1040	0.50
2 QCS groundfish	0.0343	0.80	0.0566	0.49
3 HS groundfish	0.00492	0.82	0.0030	0.52
4 WCHG groundfish	0.00160	0.79	NA	NA
5 WCVI shrimp	0.00161	1.14	0.0091	0.35
6 QCS shrimp	0.000065	2.08	0.0023	0.46
7 U.S. triennial groundfish	0.0144	1.75	0.0924	0.35

Table 12

Posterior means and coefficients of variation (CVs) of key stock assessment quantities for bocaccio (*Sebastes paucispinis*) obtained with a noninformative and informative prior for q_{gross} (see Tables 6 and 9 for the inputs for the informative prior). See Stanley et al. (2009) for the stock assessment method applied. B_{msy} (t) refers to the population biomass that provides the maximum sustainable yield in tons. B_{2008} (t) refers to the estimated population biomass in the year 2008 in tons.

	B_{msy} (t)	CV	B_{2008} (t)	CV	Replacement yield (t)	CV
Non-informative q_{gross} prior	24,146	0.68	4697	2.27	310	1.24
Informative q_{gross} prior	27,021	0.66	3022	0.83	236	0.65

it was felt that these other surveys covered most of the population's range. Also, in contrast to the present study, in these other studies it was effectively assumed that inputs were obtained from only one expert and did not formally account for cross-expert uncertainty.

All other studies so far have developed priors for q that have zero prior correlation (i.e., independence was assumed). In contrast, we developed a mixed-model structure for survey q that produces strong nonzero correlation in q_{gross} values between different surveys—a necessary consequence because the information sources used to produce the q_{gross} values for different surveys are not independent. The prior correlation between q_{gross} values for different surveys was very high in some instances (up to 0.96) because different surveys were using the same gear. This high correlation resulted in the same inputs for a given gear type feeding into the formulation of the q_{net} factor across different surveys. It is important to include this correlation in the prior for q_{gross} in a stock assessment because it accounts for the dependencies between the q_{gross} values for different surveys. Use of the marginal prior variances and assuming independence, i.e., applying zero correlation, would overstate the amount of prior information available about q_{gross}.

In contrast to the norm, of which experts tend to be overly certain, all captains in this study expressed concern about their estimates. They commented that there had been few opportunities in their careers to compare actual catches with acoustic signals for bocaccio. Three captains said that they could not provide an estimate for at least one question. All captains expressed that they would have been more comfortable estimating these values for other schooling rockfish, particularly yellowtail rockfish and widow rockfish (*S. entomelas*) because of the greater opportunity to correlate acoustic observations with observed catches. Furthermore, they commented that for bocaccio, as well as other species, catchability would be influenced by factors such as location and bottom type, time of day, state of the tide, and whether the fish were present in large schools or were solitary.

The Bayesian computations in our approach that vet the expert-specified inputs against survey-observed values for the same quantities had the result of excluding the inputs from about half of the captains. This situation is undesirable from the point of view of an attempt to include different viewpoints. However, it provides an empirical basis for screening the inputs provided by different experts. More conventional measures of experience (e.g., years of experience, total groundfish landings, and total bocaccio catch) showed either no correlation or a negative correlation with the amount of posterior weight placed on the captains. This finding indicates that practitioners should avoid applying apparently sensible criteria to formulate weights to inputs from different experts. Comparison of empirical data with the expert advice within the context of a model appears to provide a reasonably objective way of screening such advice and should be considered instead.

One of the most poorly understood parameters is the ratio of rockfish density in untrawlable to that in trawlable areas. In this analysis, a subjective prior was applied which ranged between 1 and 10, with a mode at 3. This application had the effect of reducing the central tendency of the q_{gross} by half for all surveys which would give larger estimates of population biomass. Doubling the width and mode of the input distribution for α further decreased the mean value for q_{gross}, although by no more than about 37%. We have suggested a simple Bayesian approach to updating this prior, using estimates of α from experiments. Possible approaches to estimating α could include experiments designed to estimate relative density in trawlable and untrawlable locations with gillnets, hook-and-line sampling gear, or submersible vessels (Kreiger and Sigler, 1993).

The q_{gross} prior developed for British Columbia bocaccio was applied in a recent stock assessment of this population. The availability of these priors was crucial because most of the survey index series were quite short and all had low precision. Although the prior CV was very high, i.e., no less than about 0.8, this mildly informative prior still helped to bound the range of plausible hypotheses about current stock size and replacement yield. The posterior medians for q_{gross} were also within the prior 95% PIs when a noninformative prior for it was applied, indicating that the uncertainty obtained in the priors was reasonable and that the priors were consistent with values indicated by the fit of the assessment model to the data. Thus, in this application, the method provided useful inputs for a stock assessment by bounding the range of values for estimated parameters and reducing uncertainty in key management quantities. The higher precision obtainable in stock assessment results when a noninformative prior for q is replaced with an informative prior will reduce uncertainty concerning the status of the population and allow fisheries managers to apply harvest-control measures with less uncertain consequences. With our application, less pessimistic and less imprecise assessment results could lower the risk of implementing stock rebuilding policies that would cause unnecessary hardship on the fishing industry, and larger harvests could be taken with greater confidence that they would be sustainable.

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Using productivity and susceptibility indices to assess the vulnerability of United States fish stocks to overfishing

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Abstract—Assessing the vulnerability of stocks to fishing practices in U.S. federal waters was recently highlighted by the National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration, as an important factor to consider when 1) identifying stocks that should be managed and protected under a fishery management plan; 2) grouping data-poor stocks into relevant management complexes; and 3) developing precautionary harvest control rules. To assist the regional fishery management councils in determining vulnerability, NMFS elected to use a modified version of a productivity and susceptibility analysis (PSA) because it can be based on qualitative data, has a history of use in other fisheries, and is recommended by several organizations as a reasonable approach for evaluating risk. A number of productivity and susceptibility attributes for a stock are used in a PSA and from these attributes, index scores and measures of uncertainty are computed and graphically displayed. To demonstrate the utility of the resulting vulnerability evaluation, we evaluated six U.S. fisheries targeting 162 stocks that exhibited varying degrees of productivity and susceptibility, and for which data quality varied. Overall, the PSA was capable of differentiating the vulnerability of stocks along the gradient of susceptibility and productivity indices, although fixed thresholds separating low-, moderate-, and highly vulnerable species were not observed. The PSA can be used as a flexible tool that can incorporate regional-specific information on fishery and management activity.

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The need to ascertain the status of fish stocks is a common issue for fisheries management agencies the world over. Stock assessments are usually mandated by various national or international laws and frequently include an evaluation of a stock's current biomass and fishing mortality rate compared to some reference level, often maximum sustainable yield (MSY). Because of the data requirements for evaluating the status of stocks, however, a large proportion of the world's fishery managers and scientists lack the ability to adequately assess the status of their stocks (Mora et al. 2009). In the past, many of these data-poor stocks have been managed by using a "harvest control rule" that was based on the overfishing limit for, and biomass of, the stock. However, with little knowledge of a stock's status it is difficult to appropriately apply precautionary management (Restrepo and Powers, 1999; Katsukawa, 2004). Today, however, many managers and scientists are turning to risk assessments to try to better manage stocks for which there are directed measures of stock status (e.g., Lane and Stephenson, 1998; Peterman, 2004; Fletcher et al., 2005; Astles et al., 2006).

Risk assessments for data-poor stocks usually follow some type of semiquantitative method. In previous examples of semiquantitative risk assessments, scientists have evaluated fishery impacts on bycatch and targeted species (Francis, 1992; Lane and Stephenson, 1998; Stobutzki et al., 2001a,), extinction risk (Musick, 1999; Roberts and Hawkins, 1999; Cheung et al., 2005; Mace et al., 2008), and impacts on ecosystem viability (Jennings et al., 1999; Fletcher et al., 2005; Astles et al., 2006). These approaches allow for the inclusion of less quantitative information and a wide range of factors and can complement both stock and ecosystem assessments.

In the United States, scientists of the National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration, recently developed a risk assessment to assist managers and scientists in evaluating the vulnerability of stocks to overfishing (Patrick et al., 2009). Vulnerability is a measurement of a stock's productivity and its susceptibility to a fishery. Productivity refers to the capacity of the stock to recover rapidly when depleted, whereas susceptibility is the potential for the stock to be impacted by the fishery. In general, vulnerability is an important factor to consider when organizing stock complexes, developing buffers between target and limit fishing mortality reference points, and determining which stocks should be managed under a fishery management plan. This article describes the method developed by scientists at NMFS for determining vulnerability, explores the various caveats and nuances in its underlying calculations, and presents an overview of its application to six U.S. fisheries.

Materials and methods

Determining vulnerability of stocks

Several risk assessment methods were reviewed to determine which approach would be flexible and broadly applicable across fisheries and regions. A modified version of a productivity and susceptibility analysis (PSA) was selected as the best approach for examining the vulnerability of stocks, owing to its history of use in other fisheries (Milton, 2001; Stobutzki et al., 2001a, 2001b; Braccini et al., 2006; Griffiths et al., 2006; Zhou and Griffiths, 2008) and owing to recommendations by several organizations and working groups as a reasonable approach for determining risk (Hobday et al.[1],[2]; Rosenberg et al.[3]; Smith et al., 2007).

The PSA was originally developed to classify differences in bycatch sustainability in the Australian prawn fishery (Milton, 2001; Stobutzki et al., 2001b) by evaluating the productivity (p) of bycatch stocks and their susceptibility (s) to the fishery. The values for p and s were determined by providing a score ranging from 1 to 3 for a standardized set of attributes related to each index (i.e., 7 productivity and 6 susceptibility attributes). When data were lacking, scores could be based on similar taxa or given the most vulnerable score as a precautionary approach. The scores were then averaged for each index and displayed graphically on an x-y scatter plot (Fig. 1). The two-dimensional nature of the PSA leads directly to the calculation of an overall vulnerability score (v) of a species, defined as the Euclidean distance of productivity and susceptibility scores:

$$v=\sqrt{\left[(P-X_0)^2+(S-Y_0)^2\right]}, \tag{1}$$

where x_0 and y_0 are the (x, y) origin coordinates, respectively.

Stocks that received a low productivity score and a high susceptibility score are considered to be the most vulnerable to overfishing, whereas stocks with a high productivity score and low susceptibility score are considered to be the least vulnerable.

Since 2001, the PSA has been modified by others to evaluate habitat, community, and management components of a fishery (Hobday et al.[2]; Rosenburg et al.[3]). In general, these modifications have included expanding the number of attributes for scoring, exploring additive and multiplicative models for combining scores, and examining a variety of alternative treatments for missing data. In the next section we review our application of a PSA to provide a uniform framework for evaluating the wide variety of fish stocks managed within the United States.

Identifying productivity and susceptibility attributes

With the expansion of the PSA to evaluate other management factors (e.g., habitat impacts, ecosystem considerations, management efficacy), the number of attributes that could be considered in a PSA has increased considerably—in some instances to approximately seventy-five (Hobday et al.[2]; Rosenberg et al.[3]). Although ~75 attributes have been recommended, Hobday et al.[2] noted that the use of more than six attributes per index

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[1] Hobday, A. J., A. Smith, and I. Stobutzki. 2004. Ecological risk assessment for Australian Commonwealth fisheries, 172 p. Report R01/0934 for the Australian Fisheries Management Authority, Canberra, Australia.

[2] Hobday, A. J., A. Smith, H. Webb, R. Daley, S. Wayte, C. Bulman, J. Dowdney, A. Williams, M. Sporcic, J. Dambacher, M. Fuller, T. Walker. 2007. Ecological risk assessment for the effects of fishing: methodology, 174 p. Report R04/1072 for the Australian Fisheries Management Authority, Canberra, Australia.

[3] Rosenberg, A., D. Agnew, E. Babcock, A. Cooper, C. Mogensen, R. O'Boyle, J. Powers, G. Stefansson, and J. Swasey. 2007. Setting annual catch limits for U.S. fisheries: An expert working group report, 36 p. MRAG Americas, Washington, D.C.

(e.g., productivity, susceptibility, habitat) does little to improve the accuracy of an assessment. Development of our PSA began with an initial examination and reduction of these 75 attributes to 35 after removing those perceived as redundant or not directly related to our definition of vulnerability. The remaining attributes were evaluated in two phases. In phase 1, our team provided individual scores (i.e., "yes," "no," or "maybe") to determine whether each attribute was 1) appropriate for calculating productivity or susceptibility of a stock; 2) useful at different scales (i.e., for stocks of various sizes and spatial distributions); and 3) capable of being calculated for most fisheries (i.e., for data availability). Attributes receiving a majority of "yes" scores for all three questions were retained. In phase 2, attributes receiving mixed scores, as well as new attributes not previously identified, were evaluated in a group discussion. Through this process, 18 (9 productivity, 9 susceptibility) of the 35 attributes were selected and four new attributes were added, including 1) recruitment pattern; 2) management strategy; 3) fishing rate in relation to natural mortality; and 4) desirability or value of the fishery. Overall, 22 attributes were selected for the analysis (10 productivity, 12 susceptibility). The large set of attributes to be scored, compared to previous versions of the PSA, is largely a result of the susceptibility index, including both catchability and management attributes (see *Susceptibility attributes* section below). We also recognized that the PSA would mainly be used to evaluate extremely data-poor stocks; thus, a larger set of attributes would be useful to ensure that an adequate number of attributes were scored.

Productivity attributes

Many of the productivity attributes are based on Musick's (1999) qualitative extinction risk assessment and the PSA of Stobutzki et al. (2001b). However, the scoring thresholds have been modified in many cases to better suit the distribution of life history characteristics observed in U.S. fish stocks (Table 1). Information on maximum length, maximum age, age-at-maturity, natural mortality, and von Bertalanffy growth coefficient were available for more than 140 stocks considered to be representative of U.S. fisheries (see Patrick et al., 2009). For these attributes, a range of scoring categories was evaluated by using analysis of variance (ANOVA) and *post hoc* tests to identify attribute scoring thresholds that produced significantly different bins of data. To ensure consistency in these attributes, the optimal scoring thresholds from the ANOVA were also compared to published relationships among maximum age and natural mortality (Alverson and Carney, 1975; Hoenig, 1983), von Bertalanffy growth coefficient (Froese and Binohlan, 2000), and age at maturity (Froese and Binohlan, 2000). Overall, we found this approach produced sensible categories compared to the approach of independently dividing each attribute into equal bins or using a quantile method. We defined the following 10 productivity attributes.

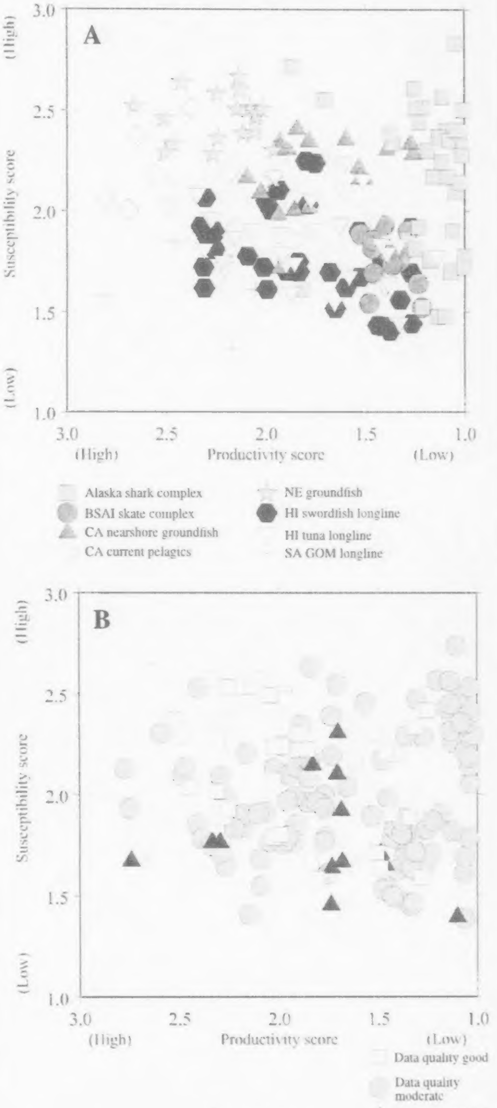

Figure 1

(**A**) Overall distribution of productivity and susceptibility x-y plot for the 166 stocks evaluated in this study, differentiated by fishery. BSAI=Bering Sea and Aleutian Islands. SA GOM= South Atlantic and Gulf of Mexico. (**B**) Associated data quality of each datum point of the 166 stocks evaluated in this study (see Appendix 1 for a list of the species in these fisheries).

Intrinsic growth rate (*r*) This is the intrinsic rate of population growth or maximum population growth that would occur in the absence of fishing at the lowest population size (Gedamke et al., 2007). Density-depen-

Table 1

Productivity attributes and rankings used to determine the vulnerability of a stock to becoming overfished.

		Ranking		
Productivity attribute	Definition	High (3)	Moderate (2)	Low (1)
r	The intrinsic rate of population growth or maximum population growth that would occur in the absence of fishing at the lowest population size.	>0.5	0.16–0.5	<0.16
Maximum age	Maximum age is a direct indication of the natural mortality rate (M), where low levels of M are negatively correlated with high maximum ages.	<10 years	10–30 years	>30 years
Maximum size	Maximum size is correlated with productivity, with large fish tending to have lower levels of productivity, although this relationship tends to degrade at higher taxonomic levels.	< 60 cm	60–150 cm	>150 cm
von Bertalanffy growth coefficient (k)	The von Bertalanffy growth coefficient measures how rapidly a fish reaches its maximum size, where long-lived, low-productivity stocks tend to have low values of k.	>0.25	0.15–0.25	<0.15
Estimated natural mortality (M)	Natural mortality rate directly reflects population productivity; stocks with high rates of natural mortality will require high levels of production in order to maintain population levels.	>0.40	0.20–0.40	<0.20
Measured fecundity	Fecundity (i.e., the number of eggs produced by a female for a given spawning event or period) is measured here at the age of first maturity.	$>10^4$	10^2–10^3	$<10^2$
Breeding strategy	The breeding strategy of a stock provides an indication of the level of mortality that may be expected for the offspring in the first stages of life.	0	1–3	≥4
Recruitment pattern	Stocks with sporadic and infrequent recruitment success often are long lived and thus may be expected to have lower levels of productivity.	Highly frequent recruitment success (>75% of year classes are successful).	Moderately frequent recruitment success (between 10% and 75% of year classes are successful).	Infrequent recruitment success (<10% of year classes are successful).
Age at maturity	Age at maturity tends to be positively related with maximum age (t_{max}); long-lived, lower productivity stocks will have higher ages at maturity than short-lived stocks.	<2 year	2–4 years	>4 years
Mean trophic level	The position of a stock within the larger fish community can be used to infer stock productivity; lower-trophic-level stocks generally are more productive than higher-trophic-level stocks.	<2.5	2.5–3.5	>3.5

dent compensation is at a maximum in these depleted conditions and therefore r is a direct measure of stock productivity. The scoring thresholds were taken from Musick (1999), who stated that r should take precedence over other productivity attributes because it combines many of the other attributes defined below.

Maximum age (t_{max}) Maximum age is related to natural mortality rate (M), where M is inversely related to maximum age (Hoenig, 1983). The scoring thresholds were based on the ANOVA applied to the observed fish stocks considered to be representative of U.S. fisheries (see Patrick et al., 2009). The t_{max} for a majority of these fish ranges between 10 and 30 years.

Maximum size (L_{max}) Maximum size is also correlated with productivity, and large fish tend to have lower levels of productivity (Roberts and Hawkins, 1999), although this relationship varies phylogenetically and is strongest within higher taxonomic levels (e.g., genus, family). The scoring thresholds were based on the ANOVA applied to the observed fish stocks considered to be representative of U.S. fisheries (see Patrick et al., 2009). The L_{max} for a majority of these fish ranges between 60 and 150 cm total length (TL).

Growth coefficient (k) The von Bertalanffy growth coefficient measures how rapidly a fish reaches its maximum size. Long-lived, low-productivity stocks tend to have low values of k (Froese and Binohlan, 2000). The scoring thresholds of 0.15 and 0.25 were based on the ANOVA applied to the observed fish stocks considered to be representative of U.S. fisheries (see Patrick et al., 2009). This observed range of k is roughly consistent with the values obtained from Froese and Binohlan's (2000) empirical relationship $k=3/\ t_{max}$ of 0.1 and 0.3, based upon t_{max} values of 10 and 30.

Natural mortality (M) Natural mortality rate directly reflects population productivity because stocks with high rates of natural mortality will require high levels of production to maintain population levels. For several methods of estimating M, one must rely on the negative relationship between M and t_{max}, including Hoenig's (1983) regression based upon empirical data, the quantile method that depends upon exponential mortality rates (Hoenig, 1983), and Alverson and Carney's (1975) relationship between mortality, growth, and t_{max}. The scoring thresholds from the ANOVA applied to the fish stocks considered to be representative of U.S. fisheries were 0.2 and 0.4, roughly consistent with those produced from Hoenig's (1983) empirical regression of 0.14 and 0.4, based on t_{max} values of 10 and 30.

Fecundity Fecundity (i.e., the number of eggs produced by a female for a given spawning event or period) varies with size and age of the spawner; therefore we followed Musick's (1999) recommendation that fecundity should be measured at the age of first maturity. As Musick (1999) noted, low values of fecundity imply low population productivity, but high values of fecundity do not necessarily imply high population productivity; thus, this attribute may be more useful at the lower fecundity values. The scoring thresholds were taken from Musick (1999) and were fecundities values of 1,000 and 100,000.

Breeding strategy The breeding strategy of a stock provides an indication of the level of mortality that may be expected for the offspring in the first stages of life. To estimate offspring mortality, we used Winemiller's (1989) index of parental investment. The index ranges from 0 to 14 and is scored according to 1) the placement of larvae or zygotes (i.e., in a nest or in the water column; score ranges from 0 to 2); 2) the length of time of parental protection of zygotes or larvae (score ranges from 0 to 4); and 3) the length of gestation period or nutritional contribution (score ranges from 0 to 8). To translate Winemiller's index into our ranking system, we examined King and McFarlane's (2003) parental investment scores for 42 North Pacific stocks. These 42 stocks covered a wide range of life histories and habitats, including 10 surface pelagic, three mid-water pelagic, three deep-water pelagic, 18 near-shore benthic, and nine offshore benthic stocks. Thirty-one percent of the stocks had a Winemiller score of zero, and 40 percent had a Winemiller score of 4 or higher; therefore 0 and 4 were used as the scoring thresholds.

Recruitment pattern Stocks with sporadic and infrequent recruitment success often are long lived and thus might be expected to have lower levels of productivity (Musick, 1999). This attribute is intended as a coarse index to distinguish stocks with sporadic recruitment patterns and high frequency of year-class failures from those with relatively steady recruitment. Thus, the proportion of years in which recruitment was above average (e.g., the percentage of successful year classes over a 10-year period) was used for this attribute. Because this attribute was viewed as a coarse index, we chose 10% and 75% as the scoring thresholds, so that scores of 1 and 3 allowed us to identify relatively extreme differences in recruitment patterns.

Age-at-maturity (t_{mat}) Age at maturity tends to be strongly related to both maximum age (t_{max}) and natural mortality (M), where long-lived, lower-productivity stocks will have higher ages at maturity than short-lived stocks (Beverton, 1992). The scoring thresholds from the ANOVA applied to the fish stocks considered to be representative of U.S. fisheries were ages 2 and 4. These values are lower than those obtained from Froese and Binohlan's (2000) empirical relationship between t_{mat} and t_{max}, which were ages 3 and 9 based upon values of t_{max} of 10 and 30. However, Froese and Binohlan (2000) used data from many fish stocks around the world, which may not be representative of U.S. stocks. For the PSA, thresholds that were obtained from the ANOVA were applied to stocks considered representative of U.S. fisheries.

Mean trophic level The position of a stock within the larger fish community can be used to infer stock productivity; lower-trophic-level stocks are generally more productive than higher-trophic-level stocks. The trophic level of a stock can be computed as a function of the trophic levels of the organisms in its diet. For this attribute, stocks with trophic levels higher than 3.5 were categorized as low-productivity stocks and stocks with trophic levels less than 2.5 were categorized as high-productivity stocks, and moderate-productivity stocks would fall between these bounds. These scoring thresholds roughly categorize piscivores to higher trophic levels, omnivores to intermediate trophic levels, and planktivores to lower trophic levels (Pauly et al., 1998) and carry the assumption that the food web analysis did not consider microbial loops as an individual trophic level.

Susceptibility attributes

Previous applications have been focused on the catchability and mortality of stocks, and other attributes, such as management effectiveness and effects of fishing gear on habitat quality, have been addressed in subsequent analyses (Hobday et al.[2]). Our susceptibility index includes all these attributes in an effort to make the results of our analysis more transparent and understandable. We defined 12 susceptibility attributes; the first seven relate to catchability and the other five measure management factors.

Like the susceptibility attributes of Hobday et al.[2], catchability attributes provide information on the likelihood of a stock's capture by a particular fishery, given the stock's range, habitat preferences, behavioral responses, and morphological characteristics that may affect its susceptibility to the fishing gear deployed in that fishery. For management attributes, one must consider how the fishery is managed: for example, fisheries with conservative management measures in place that effectively control the amount of catch are less likely to overfish. For some of these attributes, the criteria are somewhat general in order to accommodate the wide range of fisheries and management systems.

Areal overlap This attribute pertains to the extent of geographic overlap between the known distribution of a stock and the distribution of the fishery. Greater overlap implies greater susceptibility, because some degree of geographical overlap is necessary for a fishery to impact a stock. The simplest approach to determining areal overlap is to evaluate, either qualitatively or quantitatively, the proportion of the spatial distribution of a given stock that overlaps that of the fishery, based on known geographical distributions of both.

Geographic concentration Geographic concentration is the extent to which the stock is concentrated into small areas. We included this attribute because a stock with a relatively even distribution across its range may be less susceptible than a highly aggregated stock. For some species, a useful measure of this attribute is the proportion of an area of interest occupied by a specified percentage of the stock (Swain and Sinclair, 1994), which can be computed if survey data exist (see Patrick et al., 2009). For many stocks, this measure gives a general index of areal coverage that relates well to geographic concentration. However, some stocks can be concentrated in a small number of locations throughout a survey area (i.e., a "patchy" stock that is distributed over the survey area). Thus, some refinements to the index may be necessary to characterize geographic concentration in these cases.

Vertical overlap Like geographic overlap, this attribute concerns the position of the stock within the water column (e.g., demersal or pelagic) in relation to the fishing gear. Information on the depth at which gear is deployed (e.g., depth range of hooks for a pelagic longline fishery) and the depth preference of the species (e.g., obtained from archival tagging or other sources) can be used to estimate the degree of vertical overlap between fishing gear and a stock.

Seasonal migrations Seasonal migrations either to or from the fishery area (i.e., spawning or feeding migrations) could affect the overlap between the stock and the fishery. This attribute also pertains to cases where the location of the fishery changes seasonally, and therefore may be relevant for stocks captured as bycatch.

Schooling, aggregation, and other behaviors This attribute encompasses behavioral responses of both individual fish and the stock in response to fishing. Individual responses may include, for example, herding or gear-avoidance behavior that would affect catchability. An example of a population-level response is a reduction in the area of stock distribution with reduction in population size, potentially leading to increases in catchability (MacCall, 1990).

Morphological characteristics affecting capture This attribute pertains to the ability of the fishing gear to capture fish according to their morphological characteristics (e.g., body shape, spiny versus soft rayed fins). On a population level, this attribute refers to gear selectivity as it varies with fish size and age. Scoring this attribute, one should take into consideration what portion of the population size or age composition is accessible to the fishing gear or gears in question. Particular attention should be paid to the size or age at maturity in relation to capture.

Desirability or value of the fishery For this attribute, one assumes that highly valued fish stocks are more susceptible to overfishing or becoming overfished by recreational or commercial fishermen because of increased fishing effort. To identify the value of the fish, we used the price per pound or annual landings value for commercial stocks (using the higher of the two values; see Table 2) or the retention rates for recreational fisheries.

Management strategy The susceptibility of a stock to overfishing may largely depend on the effectiveness of fishery management procedures used to control catch (Roughgarden and Smith, 1996; Sethi et al., 2005; Dankel et al., 2008). Stocks managed by using catch limits that allow for fishery closure before the catch limit is exceeded (i.e., in-season or proactive accountability measures) are considered to have a low susceptibility to overfishing. Stocks managed by using catch limits and reactive accountability measures (e.g., catch levels determined after the fishing season) are considered to be moderately susceptible to overfishing or to becoming overfished. Lastly, stocks that have neither catch limits nor accountability measures are considered to be highly susceptible to overfishing.

Fishing mortality rate (in relation to M) This attribute is applicable to stocks for which estimates of both fishing and natural mortality rates (F and M) are available. Because sustainable fisheries management typically involves conserving the reproductive potential of a stock, it is recommended that the average F on mature fish be used where possible, as opposed to the fully selected or "peak" F. We base our thresholds on the conservative rule of thumb that the M should be an upper limit of F (Thompson, 1993), and thus F/M should not exceed 1. For this attribute, we define intermediate F/M values as those between 0.5 and 1.0; values above 1.0 and below 0.5 are defined as high and low susceptibility, respectively.

Biomass of spawners Analogous to fishing mortality rate, a comparison of the current stock biomass ($B_{CURRENT}$) to expected unfished levels (B_0) offers information on the extent to which fishing has potentially depleted the stock and the stock's realized susceptibility to overfishing. If B_0 is not available, one could compare $B_{CURRENT}$ against the maximum observed biomass from a time series of population size estimates (e.g., from a research survey). If a time series is used, it should be of adequate length, and it should be recognized that the maximum observed survey estimates may not correspond to the true maximum biomass and that substantial observation errors in estimates may be present. Additionally, stocks may decline in abundance because of environmental factors unrelated to their susceptibility to the fishery, and therefore this situation should be considered by scientists when evaluating depletion estimates. Notwithstanding these issues, which can be addressed with the data quality score described below, some measure of current stock abundance was viewed as a useful attribute.

Survival after capture and release Fish survival after capture and release varies by species, region, depth, gear type, and even market conditions, and thus can affect the susceptibility of the stock (Davis, 2002). Considerations of barotraumatic effects, discarding methods, and gear invasiveness (e.g., gears with hooks or nets would likely be more invasive than traps) are particularly relevant.

Fishery impact on habitat A fishery may have an indirect effect on a species through adverse impacts on habitat (Benaka, 1999; Barnes and Thomas, 2005). Within the United States, a definition of the level of impact is the focus of environmental impact statements and essential fish habitat evaluations (see Rosenberg et al., 2000). To align with NMFS evaluations of impact, the scoring thresholds for this attribute were categorized as minimal, temporary, or mitigated.

Defining attribute scores and weights

Depending on the specific stock being evaluated, not all of the productivity and susceptibility attributes listed in Tables 1 and 2 will be equally useful in determining the vulnerability of a stock. In previous versions of the PSA, an attribute weighting scheme was used in which higher weights were applied to the more important attributes (Stobutzki et al., 2001b; Hobday et al.[1]; Rosenberg et al.[3]). We used a default weight of 2 for the productivity and susceptibility attributes, where attribute weights can be adjusted within a scale from 0 to 4 to customize the application to each fishery. In determining the proper weighting of each attribute, users should consider the relevance of the attribute for describing productivity or susceptibility rather than the availability of data for that attribute (e.g., data-poor attributes should not automatically receive low weightings). In some rare cases, it is also anticipated that some attributes will receive a weighting of zero, which cause them to be removed from the analysis, because the attribute has no relation to the fishery and its stocks. Some attributes (e.g., management strategy, fishing mortality rate, biomass of spawners, etc.) may also be removed from the analysis to avoid double-counting if they are considered in a more overarching risk analysis, for which the results of the PSA are only one component.

Like Milton (2001) and Stobutzki et al. (2001b), we defined the criteria for a score of 1, 2, or 3 to a productivity or susceptibility attribute (see Table 1). However, our approach provides users the flexibility to apply intermediate scores (e.g., 1.5 or 2.5) when the attribute value spans two categories. Owing to the subjective nature of semiquantitative analyses, scores should be applied in a consistent manner to reduce scoring bias (Lichtensten and Newman, 1967; Janis, 1983; Von Winterfeldt and Edwards, 1986; Bell et al., 1988), such as by employing the Delphi method (see Okoli and Pawlowski, 2004 and Landeta, 2006).

Data-quality index

As a precautionary measure for risk assessment scoring, the highest-level risk score can be used when data are missing to account for uncertainty and to avoid identifying a high-risk stock as low risk (Hardwood, 2000; Milton, 2001; Stobutzki et al., 2001b; Astles et al., 2006). Although precautionary, that approach also confounds the issues of data quality with risk assessment. For example, a data-poor stock may receive

Table 2

Susceptibility attributes and rankings used to determine the vulnerability of a stock becoming overfished.

Susceptibility attribute	Definition
Areal overlap	The extent of geographic overlap between the known distribution of a stock and the distribution of the fishery.
Geographic concentration	The extent to which the stock is concentrated into small areas.
Vertical overlap	The position of the stock within the water column (i.e., whether is demersal or pelagic) in relation to the fishing gear.
Seasonal migrations	Seasonal migrations (i.e. spawning or feeding migrations) either to or from the fishery area could affect the overlap between the stock and the fishery.
Schooling, aggregation, and other behavioral responses	Behavioral responses of both individual fish and the stock in response to fishing.
Morphological characteristics affecting capture	The ability of the fishing gear to capture fish based on their morphological characteristics (e.g., body shape, spiny versus soft rayed fins, etc.).
Desirability or value of the fishery	The assumption that highly valued fish stocks are more susceptible to overfishing or to becoming overfished by recreational or commercial fishermen owing to increased effort.
Management strategy	The susceptibility of a stock to overfishing may largely depend on the effectiveness of fishery management procedures used to control catch.
Fishing rate relative to *M*	As a conservative rule of thumb, it is recommended that *M* should be the upper limit of *F* so as to conserve the reproductive potential of a stock.
Biomass of spawners (SSB) or other proxies	The extent to which fishing has depleted the biomass of a stock in relation to expected unfished levels offers information on realized susceptibility.
Survival after capture and release	Fish survival after capture and release varies by species, region, and gear type or even market conditions, and thus can affect the susceptibility of the stock.
Impact of fisheries on essential fish habitat or habitat in general for nontargeted fish	A fishery may have an indirect effect on a species by adverse impacts on habitat.

a high-risk evaluation either from an abundance of missing data or from the risk assessment of the available data, with the result that the risk scores may be inflated (Hobday et al.[1]). In contrast, we considered missing data within the larger context of data quality, and report the overall quality of data as a separate value.

A data-quality index was developed to represent the information quality of individual vulnerability scores based on five tiers, ranging from best data (or high belief in the score) to no data (or little belief in the score) (Table 3). The data-quality score is computed for the productivity and susceptibility scores as a weighted average and implies the overall quality of the data or belief in the score rather than the actual type of data used in the analysis. Like Hobday et al.[2], we divided the data-quality scores into three groupings (poor >3.5; moderate 2.0–3.5; and good <2.0) for display purposes. This information, along with more detailed descriptions of data quality (e.g., mean score, range), is a quick and useful means of providing decision-makers with details on the uncertainty of the vulnerability

Ranking		
Low (1)	Moderate (2)	High (3)
<25% of stock present in the area fished.	Between 25% and 50% of the stock present in the area fished.	>50% of stock present in the area fished.
Stock is distributed in >50% of its total range	Stock is distributed in 25% to 50% of its total range	Stock is distributed in <25% of its total range.
<25% of stock present in the depths fished.	Between 25% and 50% of the stock present in the depths fished.	>50% of stock present in the depths fished
Seasonal migrations decrease overlap with the fishery.	Seasonal migrations do not substantially affect the overlap with the fishery.	Seasonal migrations increase overlap with the fishery.
Behavioral responses of fish decrease the catchability of the gear.	Behavioral responses of fish do not substantially affect the catchability of the gear.	Behavioral responses of fish increase the catchability of the gear (i.e., hyperstability of catch per unit of effort with schooling behavior).
Species shows low susceptibility to gear selectivity.	Species shows moderate susceptiblity to gear selectivity.	Species shows high susceptiblity to gear selectivity.
Stock is not highly valued or desired by the fishery (<\$1/lb; <\$500K/yr landed; <33% retention).	Stock is moderately valued or desired by the fishery (\$1–\$2.25/lb; \$500K–\$10,000K/yr landed; 33–66% retention).	Stock is highly valued or desired by the fishery (>\$2.25/lb; >\$10,000K/yr landed; >66% retention).
Targeted stocks have catch limits and proactive accountability measures; nontarget stocks are closely monitored.	Targeted stocks have catch limits and reactive accountability measures.	Targeted stocks do not have catch limits or accountability measures; nontargeted stocks are not closely monitored.
<0.5	0.5–1.0	>1
B is >40% of B_0 (or maximum observed from time series of biomass estimates).	*B* is between 25% and 40% of B_0 (or maximum observed from time series of biomass estimates).	*B* is <25% of B_0 (or maximum observed from time series of biomass estimates).
Probability of survival >67%	33% < probability of survival <67%	Probability of survival <33%
Adverse effects absent, minimal or temporary.	Adverse effects more than minimal or temporary but are mitigated.	Adverse effects more than minimal or temporary and are not mitigated.

scores. Such uncertainty in the data would help with the interpretation of the overall vulnerability score and also help in targeting areas of further research and data needs.

Example case studies

To demonstrate the utility of our PSA scoring process, we evaluated six U.S. fisheries including the Northeast groundfish multispecies, highly migratory Atlantic shark complexes, California nearshore groundfish finfish assemblage, California Current coastal pelagic species, skates of the Bering Sea and Aleutian Islands (BSAI) management area (a bycatch fishery of the BSAI groundfish fishery), and the Hawaii-based pelagic longline fishery (both the tuna and swordfish sectors). In total, 162 stocks were evaluated (Appendix 1). These fisheries were chosen because they were expected to display varying degrees of productivity, susceptibility, and data quality. For descriptions of these fisheries and details on how our PSA scoring procedure was applied to each fishery, see Patrick et al. (2009).

Table 3

The five tiers of data quality used when evaluating the productivity and susceptibility of an individual stock.

Data quality tier	Description	Example
1	Best data. Information is based on collected data for the stock and area of interest that is established and substantial	Data-rich stock assessment; published literature for which multiple methods are used, etc.
2	Adequate data Information is based on limited coverage and corroboration, or for some other reason is deemed not as reliable as tier-1 data	Limited temporal or spatial data, relatively old information, etc.
3	Limited data. Estimates with high variation and limited confidence and may be based on studies of similar taxa or life history strategies	Similar genus or family, etc.
4	Very limited data. Information based on expert opinion or on general literature reviews from a wide range of species, or outside of region	General data not referenced
5	No data. When there are no data on which to make even an expert opinion, the person using the PSA should give this attribute a "data quality" score of 5 and not provide a "productivity" or "susceptibility" score so as not to bias those index scores. When plotted, the susceptibility or productivity index score will be based on one less attribute, and will be highlighted as such by its related quality score.	

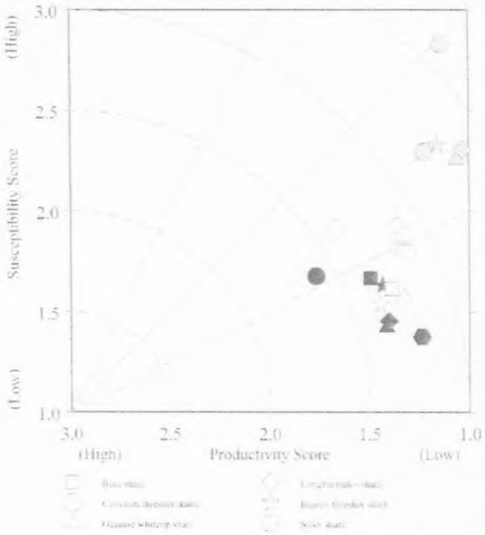

Figure 2

Comparison of vulnerabilities among common shark species in the highly migratory Atlantic shark complexes (gray), Hawaii-based pelagic longline—tuna sector (white), and Hawaii-based pelagic longline—swordfish sector (black).

Results and discussion

Range of vulnerability scores

The managed stocks evaluated in this report represent both targeted (n=71; 44%) and nontargeted species (n=91; 56%) that were included in fishery management plans to prevent overfishing and rebuild overfished stocks. The stocks generally displayed vulnerability scores greater than 1.0 (Fig. 1). Species evaluated within the Atlantic highly migratory shark complexes were found to be the most vulnerable, averaging vulnerability scores of 2.17, and California Current coastal pelagic species were the least vulnerable, averaging 1.29.

Although different groups of species will exhibit different ranges of productivity and susceptibility scores, it is interesting to note that in some cases even the same species may exhibit different productivity scores. For example, the productivity scores for the blue (*Prionace glauca*), bigeye thresher (*Alopias superciliosus*), longfin mako (*Isurus paucus*), oceanic whitetip (*Carcharhinus longimanus*), silky (*C. falciformis*), and common thresher (*A. vulpinus*) sharks differed between the highly migratory Atlantic shark complexes and the Hawaii-based pelagic longline fishery example applications (Fig. 2). These differences are likely related to intraspecific variations in life history patterns (Cope, 2006) and to the use of different weightings in the vulnerability analysis (see Patrick et al., 2009).

In contrast, the species in the Hawaii-based pelagic longline fishery (both the tuna and swordfish sectors) showed an expanded range of productivity and suscep-

Table 4

Summary of the productivity and susceptibility scoring frequencies and correlations to the overall index or category score. Correlations were based on stock attributes scores (1–3) (see Tables 1 and 2) that were compared to a modified categorical score for the stock, the latter of which did not include the related attribute score.

Category	No. scored	Frequency scored	Pearson correlation coefficient	P-value
Productivity				
r	128	96%	0.596	<0.001
Maximum age	126	95%	0.674	<0.001
Maximum size	128	96%	0.592	<0.001
von Bertalanffy growth coefficient (k)	129	97%	0.656	<0.001
Estimated natural mortality (M)	127	95%	0.785	<0.001
Measured fecundity	126	95%	0.509	<0.001
Breeding strategy	133	100%	0.568	<0.001
Recruitment pattern	84	63%	−0.211	0.054
Age at maturity	125	94%	0.802	<0.001
Mean trophic level	132	99%	0.439	<0.001
Susceptibility				
Catchability				
Areal overlap	123	92%	0.333	<0.001
Geographic concentration	133	100%	0.345	<0.001
Vertical overlap	133	100%	0.772	<0.001
Seasonal migrations	49	37%	0.058	0.692
Schooling, aggregation, and other behavioral responses	87	65%	0.340	0.001
Morphology affecting capture	132	99%	0.319	<0.001
Desirability or value of the fishery	133	100%	0.504	<0.001
Management				
Management strategy	133	100%	0.154	0.077
Fishing rate in relation to M	79	59%	0.510	<0.001
Biomass of spawners (SSB) or other proxies	78	59%	0.389	<0.001
Survival after capture and release	126	95%	0.201	0.024
Fishery impact to essential fish habitat (EFH) or habitat in general for nontargeted fish	133	100%	0.286	0.001

tibility scores. The swordfish sector overall exhibited a slightly reduced susceptibility when compared to the tuna sector, probably due to the higher level of targeting in the tuna sector of the fishery (Fig. 1). The restricted range in some of the example applications may reflect the species chosen for these examples, and a more expanded range may be observed if the PSA were applied to all species in a fishery management plan (FMP). For example, BSAI skate complexes are managed as bycatch within the BSAI Groundfish FMP, which includes a range of life-history types, including rockfish and flatfish, and the productivity and susceptibility scores for these species would likely contrast with those obtained for skates.

A restricted range of scores from a PSA may motivate some to modify the attribute scoring thresholds to produce greater contrast. But because the overall goal of the present PSA is to estimate vulnerability in relation to an overall standard appropriate for the range of managed species, a lack of contrast in vulnerability scores may simply reflect a limited breadth of species diversity. It may be advantageous in some cases to modify the attribute scoring thresholds to increase the contrast within a given region or FMP (see Field et al., in press), while recognizing that the vulnerability scores for that particular fishery no longer represent the risk of overfishing based on the original scoring criteria described here.

Data availability and data quality

From our example applications, data availability was relatively high for the majority of the attributes evaluated, averaging 88% and ranging from 37% to 100% in scoring frequency (Table 4). However, the quality of these data was considered moderate (i.e., medium data quality scores of 2–3), except for the Northeast multispecies groundfish fishery (Fig. 1). The high degree of data quality for those targeted stocks reflects the relatively long time series of fishery and survey data. In general, a relationship between susceptibility and data quality is intuitive (i.e., valuable stocks are likely the most susceptible owing to targeting, and priority is therefore given to the collection of data for valuable target fisheries).

The degree of consistency within the productivity and susceptibility scores was determined from correlations of a particular attribute to its overall productivity or susceptibility score (after removal of the attribute being evaluated). In this analysis, susceptibility attributes related to management were separated from other susceptibility attributes. All but two of the attributes had relatively high correlation coefficients, with an overall average correlation of 0.43 and ranging from −0.21 to 0.80 (Table 4). The correlation coefficients for recruitment pattern (−0.21) and seasonal migration (0.06) were unusually low and could reflect the narrow range of observed recruitment patterns or seasonal migrations, as is evident from each attribute being scored 90% of the time as a moderate risk. Although these attributes were not informative for the majority of the stocks we examined, we anticipate that these attributes may prove to be more useful for other fisheries. As previously noted, in these cases the attribute weight can be adjusted to reflect its utility.

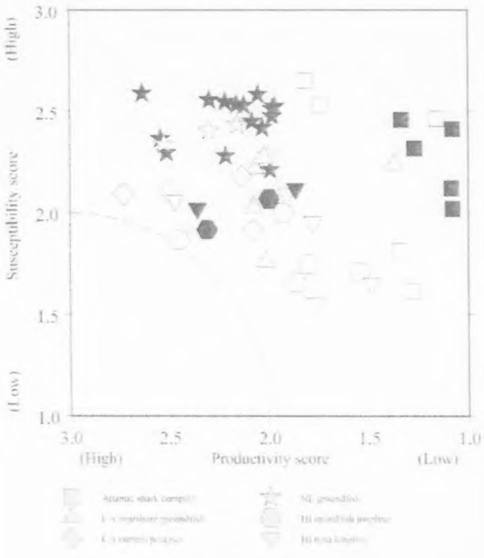

Figure 3

A subset of the stocks from the example applications (n=50) for which the status (stock is either overfished [$F_{CURRENT}>F_{MSY}$] or is being overfished [$B_{CURRENT}<B_{MSY}$]) could be determined between 2000 and 2008. Productivity and susceptibility analysis scores increase with distance from the origin, as does the vulnerability score. The dashed line references the minimum vulnerability scores observed among the 162 stocks evaluated in the applications.

Relationship of stock vulnerability to fishing pressure

To evaluate the efficacy of the PSA in identifying stocks that are vulnerable to overfishing, we examined a subset ($n=50$) of the example stocks for which status determination criteria were available to assess whether the stock's maximum sustainable fishing mortality rate (i.e., whether it is being overfished) or minimal stock size threshold (i.e., whether it was overfished) had been exceeded between the years of 2000 and 2008 (Fig. 3). Kruskal-Wallis tests indicated significant differences in susceptibility ($P=0.001$) and vulnerability ($P=0.002$) scores between stocks that had been overfished or that were being overfished in the past (i.e., Northeast groundfish multispecies and highly migratory Atlantic shark complexes) and those that had not. However, productivity scores were not found to be significantly different ($P=0.891$). Stocks that had been overfished or that were being overfished in the past generally had susceptibility scores greater than 2.3 and vulnerability scores greater than 1.8.

To further examine the efficacy of the PSA to identify vulnerable stocks, we evaluated four lightly fished nontarget species (i.e., minor bycatch species) that were unlikely to be impacted by fishing activities in their region according to their average landings (<5 metric tons/yr), price value (<$1.00/lb), and suspected high productivity rates. These minor bycatch species, from the South Atlantic and Gulf of Mexico snapper-grouper longline fishery, represented stocks that should have substantially lower vulnerability scores (<1.0) compared to the other species that are considered either targeted species or major bycatch species. Three of the four nontarget species received vulnerability scores of less than 1.0 (Fig. 1), but the other stock (sand tilefish, *Malacanthus plumieri*) received a vulnerability score of 1.1 because of its moderate productivity (2.1) and susceptibility (1.9).

These *post hoc* results involving stocks with status determinations and lightly fished nontarget species, although limited, indicate that the PSA can differentiate between low- and highly vulnerable stocks. However, a fixed threshold for delineating between the varying levels of vulnerability was not observed in all situations because a gradient of vulnerabilities existed. Therefore, determination of appropriate thresholds for low-, moderate-, and highly vulnerable stocks will likely reflect the nature of each particular fishery and the management action that will be applied. In some cases, managers may prefer to use the results of the PSA in a contextual or qualitative manner to determine management decisions rather than as a basis for specifying rigid decision rules. When thresholds are desired, we recommend that managers and scientists jointly determine appropriate thresholds on a fishery-by-fishery basis.

Comparisons between target and nontarget stocks

Comparisons of productivity and susceptibility between target and nontarget stocks were made in the Hawaii-

Table 5

Nonparametric statistical analysis of targeted versus non-targeted species productivity, susceptibility, and vulnerability scores in the highly migratory Atlantic shark complexes and Hawaii-based pelagic longline sector fisheries.

		Kruskal-Wallis P-values		
Fishery	Number	Productivity	Susceptibility	Vulnerability
Hawaii-based pelagic longline—tuna	33	0.026	0.373	0.072
Hawaii-based pelagic longline—swordfish	33	0.026	0.153	0.058
Highly migratory Atlantic shark complexes	37	0.150	<0.001	0.380
Combined	103	0.752	<0.001	0.160

based pelagic longline (tuna sector), Hawaii-based pelagic longline (swordfish sector), and the highly migratory Atlantic shark complexes (nontarget stocks are identified in Appendix 1). Kruskall-Wallis tests revealed that the productivity scores were significantly different between the target and nontarget stocks in each of the two sectors of the Hawaii-based pelagic longline fishery ($P=0.026$), whereas the susceptibility scores were significantly different ($P<0.001$) in the highly migratory Atlantic shark complexes (Table 5). None of these cases showed significant differences in both axes, and no significant differences were observed in vulnerability. Like others, these results indicate that nontarget stocks can be as vulnerable to overfishing as the target stocks of a fishery and reinforce the need for a careful examination of the vulnerability of nontarget stocks when making management decisions (see Alverson et al., 1994; Hall, 1996; Kaiser and de Groot, 2000).

Conclusions

Although many qualitative risk analyses are used by fisheries scientists and managers, the PSA is a particularly useful method for determining vulnerability because it permits an evaluation of both the productivity of the stock and its susceptibility to the fishery. The output from this relatively simple and straightforward tool provides managers and scientists an index of how vulnerable target and nontarget stocks within a fishery are to becoming overfished. Even when specific values for many life history parameters are not well known, the categorical bins of low, medium, and high values are often distinct enough to allow scores for even the most data-poor species. The bins also help in determining the needed strength of conservation measures and the degree of precaution to apply in management measures. They can also identify those stocks or fisheries that warrant further, more complicated analytical attention.

Our analyses indicate that the PSA is generally capable of distinguishing the vulnerability of stocks that experience differing levels of fishing pressure, although fixed thresholds separating low-, medium-, and high-vulnerability stocks were not developed. When fixed thresholds of vulnerability are desired, it is recommended that managers and scientists determine thresholds between low-, medium-, and high-vulnerability stocks on a fishery-by-fishery basis, using cluster analysis or other techniques that identify groups of similar species.

Like those of Shertzer and Williams (2008), our example applications showed that current stock complexes exhibit a wide range of vulnerabilities (e.g., highly migratory Atlantic shark complexes). Therefore, managers should consider reorganizing complexes that exhibit a wide range of vulnerabilities, or at least consider choosing an indicator stock that represents the more vulnerable stock(s) within the complex. If an indicator stock is found to be less vulnerable than other members of the complex, management measures should be conservative so that the more vulnerable members of the complex are not at risk from the fishery.

It is also important to note that PSA scores will likely vary between sectors of a targeted fishery (e.g., gear type, user group) or among fisheries that capture the stock as bycatch. For example, the susceptibility score for "survival after capture and release" may differ greatly between trawl and gill net gears. Thus, it is recommended that a vulnerability evaluation be performed for all or a majority of sectors interacting with the stock when the overall vulnerability of stock is needed (e.g., for setting control rule buffers, identifying sectors where stocks are particularly vulnerable, etc.). An overarching vulnerability evaluation score could then be calculated by using a weighting system based on average landings by sector over some predetermined time frame.

Scientists have begun using the PSA in developing control rules for fisheries management. For example, the South Atlantic Fishery Management Council is considering an acceptable biological catch control rule that is based on a tiered system that reduces the probability of overfishing from 50% (i.e., the overfishing limit) to as low as 20% based on 1) the uncertainty in the stock assessment, 2) the status of the stock, and 3) the vulnerability score from the PSA (SAFMC[4]). Additional control rule frameworks are being developed within NMFS (Witherell[5]). We assert that as fishery scientists and management advisors begin to explore the use of risk analysis, that the PSA is one approach that could demonstrably help managers to make more informed decisions, particularly in instances where data are limited.

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Appendix 1

List of example stocks and associated fisheries used to evaluate the efficacy of the productivity and susceptibility indices in determining vulnerability of stocks to becoming overfished.

Fishery	Stock	Scientific name
Highly migratory Atlantic shark complexes	Sixgill shark*	*Hexanchus griseus*
	Sharpnose sevengill shark*	*Heptranchias perlo*
	Bigeye sandtiger shark*	*Odontaspis noronhai*
	Whale shark*	*Rhincodon typus*
	Caribbean sharpnose shark*	*Rhizoprionodon porosus*
	Angel shark*	*Squatina dumeril*
	White shark*	*Carcharodon carcharias*
	Basking shark*	*Cetorhinus maximus*
	Sandtiger shark*	*Carcharias taurus*
	Blue shark*	*Prionace glauca*
	Smalltail shark*	*Carcharhinus porosus*
	Nurse shark	*Ginglymostoma cirratum*
	Galapagos shark*	*Carcharhinus galapagensis*
	Dusky shark*	*Carcharhinus obscurus*
	Porbeagle*	*Lamna nasus*
	Common thresher shark*	*Alopias vulpinus*
	Oceanic whitetip shark*	*Carcharhinus longimanus*
	Blacknose shark	*Carcharhinus acronotus*
	Lemon shark	*Negaprion brevirostris*
	Shortfin mako*	*Isurus oxyrinchus*
	Longfin mako*	*Isurus paucus*
	Tiger shark	*Galeocerdo cuvier*
	Smooth hammerhead shark	*Sphyrna zygaena*
	Caribbean reef shark*	*Carcharhinus perezi*
	Blacktip shark	*Carcharhinus limbatus*
	Scalloped hammerhead shark	*Sphyrna lewini*
	Sandbar shark	*Carcharhinus plumbeus*
	Bigeye thresher shark*	*Alopias superciliosus*
	Finetooth shark	*Carcharhinus isodon*
	Night shark*	*Carcharhinus signatus*
	Bignose shark*	*Carcharhinus altimus*
	Bonnethead shark	*Sphyrna tiburo*
	Spinner shark	*Carcharhinus brevipinna*
	Bull shark	*Carcharhinus leucas*
	Great hammerhead shark	*Sphyrna mokarran*
	Atlantic sharpnose shark	*Rhizoprionodon terraenovae*
	Silky shark	*Carcharhinus falciformis*
Bering Sea and Aleutian Islands skate complexes	Alaska skate*	*Bathyraja parmifera*
	Aleutian skate*	*Bathyraja aleutica*
	Commander skate*	*Bathyraja lindbergi*
	Whiteblotched skate*	*Bathyraja maculata*
	Whitebrow skate*	*Bathyraja minispinosa*
	Roughtail skate*	*Bathyraja trachura*
	Bering skate*	*Bathyraja interrupta*
	Mud skate*	*Bathyraja taranetzi*
	Roughshoulder skate*	*Amblyraja badia*
	Big skate*	*Raja binoculata*
	Longnose skate*	*Raja rhina*
	Butterfly skate*	*Bathyraja mariposa*
	Deepsea skate*	*Bathyraja abyssicola*
California nearshore groundfish finfish assemblage	California sheephead	*Semicossyphus pulcher*
	Cabezon	*Scorpaenichthys marmoratus*
	Kelp greenling	*Hexagrammos decagrammus*

continued

Appendix 1 (continued)

Fishery	Stock	Scientific name
California nearshore groundfish finfish assemblage (cont.)	Rock greenling	*Hexagrammos lagocephalus*
	California scorpionfish	*Scorpaena guttata*
	Monkeyface prickelback	*Cebidichthys violaceus*
	Black rockfish	*Sebastes melanops*
	Black-and-yellow rockfish	*Sebastes chrysomelas*
	Blue rockfish	*Sebastes mystinus*
	Brown rockfish	*Sebastes auriculatus*
	Calico rockfish*	*Sebastes dallii*
	China rockfish	*Sebastes nebulosus*
	Copper rockfish	*Sebastes caurinus*
	Gopher rockfish	*Sebastes carnatus*
	Grass rockfish	*Sebastes rastrelliger*
	Kelp rockfish	*Sebastes atrovirens*
	Olive rockfish	*Sebastes serranoides*
	Quillback rockfish	*Sebastes maliger*
	Treefish rockfish	*Sebastes serriceps*
California Current coastal pelagic species	Pacific sardine	*Sardinops sagax*
	Northern anchovy	*Engraulis mordax*
	Pacific mackerel	*Scomber japonicus*
	Jack mackerel	*Trachurus symmetricus*
	Market squid	*Doryteuthis opalescens*
	Pacific herring	*Clupea pallasii*
	Pacific bonito	*Sarda chiliensis*
	Pacific saury	*Cololabis saira*
Northeast groundfish multispecies	Gulf of Maine cod	*Gadus morhua*
	Georges Bank cod	*Gadus morhua*
	Gulf of Maine haddock	*Melanogrammus aeglefinus*
	Georges Bank haddock	*Melanogrammus aeglefinus*
	Redfish	*Sebastes marinus*
	Pollock	*Pollachius virens*
	Cape Cod/Gulf of Maine yellowtail flounder	*Limanda ferruginea*
	Georges Bank yellowtail flounder	*Limanda ferruginea*
	Southern New England yellowtail flounder	*Limanda ferruginea*
	American plaice	*Hippoglossoides platessoides*
	Witch flounder	*Glyptocephalus cynoglossus*
	Gulf of Maine Winter flounder	*Pseudopleuronectes americanus*
	Georges Bank Winter flounder	*Pseudopleuronectes americanus*
	Southern New England/Mid-Atlantic winter flounder	*Pseudopleuronectes americanus*
	Gulf of Maine/Georges Bank windowpane	*Scophthalmus aquosus*
	Southern New EnglandMid-Atlantic windowpane	*Scophthalmus aquosus*
	Ocean pout	*Zoarces americanus*
	White hake	*Urophycis tenuis*
	Atlantic halibut	*Hippoglossus hippoglossus*
Hawaii-based pelagic longline—swordfish	Albacore	*Thunnus alalunga*
	Bigeye tuna	*Thunnus obesus*
	Black marlin*	*Makaira indica*
	Bullet tuna	*Auxis rochei rochei*
	Pacific pomfret*	*Brama japonica*
	Blue shark*	*Prionace glauca*
	Bigeye thresher shark*	*Alopias superciliosus*
	Blue marlin*	*Makaira mazara*
	Dolphin fish (mahi mahi)*	*Coryphaena hippurus*
	Brilliant pomfret*	*Eumegistus illustris*
	Kawakawa*	*Euthynnus affinis*
	Spotted moonfish*	*Lampris guttatus*
	Longfin mako shark*	*Isurus paucus*

continued

Appendix 1 (continued)

Fishery	Stock	Scientific name
Hawaii-based pelagic longline—swordfish (cont.)	Salmon shark*	*Lamna ditropis*
	Striped marlin*	*Tetrapturus audax*
	Oilfish*	*Ruvettus pretiosus*
	Northern bluefin tuna*	*Thunnus orientalis*
	Roudi escolar*	*Promethichthys prometheus*
	Pelagic thresher shark*	*Alopias pelagicus*
	Sailfish*	*Istiophorus platypterus*
	Skipjack tuna	*Katsuwonus pelamis*
	Shortfin mako shark*	*Isurus oxyrinchus*
	Shortbill spearfish*	*Tetrapturus angustirostris*
	Broad billed swordfish	*Xiphias gladius*
	Flathead pomfret*	*Taractichthys asper*
	Dagger pomfret*	*Taractichthys rubescens*
	Sickle pomfret*	*Taractichthys steindachneri*
	Wahoo*	*Acanthocybium solandri*
	Yellowfin tuna	*Thunnus albacares*
	Oceanic whitetip shark*	*Carcharhinus longimanus*
	Silky shark*	*Carcharhinus falciformis*
	Common thresher shark*	*Alopias vulpinus*
	Escolar*	*Lepidocybium flavobrunneum*
Hawaii-based pelagic longline—tuna	Albacore	*Thunnus alalunga*
	Bigeye tuna	*Thunnus obesus*
	Black Marlin*	*Makaira indica*
	Bullet tuna	*Auxis rochei rochei*
	Pacific pomfret*	*Brama japonica*
	Blue Shark*	*Prionace glauca*
	Bigeye thresher shark*	*Alopias superciliosus*
	Blue marlin*	*Makaira mazara*
	Dolphin fish (mahi mahi)*	*Coryphaena hippurus*
	Brilliant pomfret*	*Eumegistus illustris*
	Kawakawa*	*Euthynnus affinis*
	Spotted moonfish*	*Lampris guttatus*
	Longfin mako shark*	*Isurus paucus*
	Salmon shark*	*Lamna ditropis*
	Striped marlin*	*Tetrapturus audax*
	Oilfish*	*Ruvettus pretiosus*
	Northern bluefin tuna*	*Thunnus orientalis*
	Roudi escolar*	*Promethichthys prometheus*
	Pelagic thresher shark*	*Alopias pelagicus*
	Sailfish*	*Istiophorus platypterus*
	Skipjack tuna	*Katsuwonus pelamis*
	Shortfinned mako shark*	*Isurus oxyrinchus*
	Short bill spearfish*	*Tetrapturus angustirostris*
	Broad billed swordfish*	*Xiphias gladius*
	Flathead pomfret*	*Taractichthys asper*
	Dagger pomfret*	*Taractichthys rubescens*
	Sickle pomfret*	*Taractichthys steindachneri*
	Wahoo*	*Acanthocybium solandri*
	Yellowfin tuna	*Thunnus albacares*
	Oceanic whitetip shark*	*Carcharhinus longimanus*
	Silky shark*	*Carcharhinus falciformis*
	Common thresher shark*	*Alopias vulpinus*
	Escolar*	*Lepidocybium flavobrunneum*
South Atlantic and Gulf of Mexico snapper-grouper longline	Sand tilefish*	*Malacanthus plumieri*
	Rock sea bass*	*Centropristis philadelphica*
	Margate*	*Haemulon album*
	Bar jack*	*Caranx ruber*

*Nontarget stocks.

Distribution and life history of two diminutive flatfishes, *Citharichthys gymnorhinus* and *C. cornutus* (Pleuronectiformes: Paralichthyidae), in the western North Atlantic

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Abstract—*Citharichthys cornutus* and *C. gymnorhinus*, diminutive flatfishes inhabiting continental shelves in the western Atlantic Ocean, are infrequently reported and poorly known. We identified 594 *C. cornutus* in 56 different field collections (68–287 m; most between 101–200 m) off the eastern United States, Bahamas, and eastern Caribbean Sea. Historical records and recently captured specimens document the northern geographic range of adults on the shelf off New Jersey (40°N, 70°W). *Citharichthys cornutus* measured 17.2–81.3 mm standard length (SL); males (20.0–79.1 mm SL) and females (28.0–81.3 mm SL) attain similar sizes (sex could not be determined for fish <20 mm SL). Males reach nearly 100% maturity at ≥60 mm SL. The smallest mature females are 41.5 mm SL, and by 55.1 mm SL virtually all are mature. Juveniles are found with adults on the outer shelf. Only 214 *C. gymnorhinus* were located in 42 different field collections (35–201 m, with 90% between 61 and 120 m) off the east coast of the United States, Bahamas, and eastern Caribbean Sea. Adults are found as far north as the shelf off Cape Hatteras, NC (35°N, 75°W). This diminutive species (to 52.4 mm SL) is among the smallest flatfishes but males (n=131; 20.3–52.4 mm SL) attain a slightly larger maximum size than that of females (n=58; 26.2–48.0 mm SL). Males begin to mature between 29 and 35 mm SL and reach 100% maturity by 35–40 mm SL. Some females are mature at 29 mm SL, and all females >35.1 mm SL are mature. Overlooked specimens in museum collections and literature enabled us to correct long-standing inaccuracies in northern distributional limits that appear in contemporary literature and electronic data bases for these species. Associated locality-data for these specimens allow for proper evaluation of distributional information for these species in relation to hypotheses regarding shifts in species ranges due to climate change effects.

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Citharichthys cornutus (Günther, 1880), the horned whiff, and *C. gymnorhinus* Gutherz and Blackman, 1970, the anglefin whiff, are small-size, poorly known flatfishes inhabiting substrata located on the middle and outer continental shelves— primarily in subtropical and tropical waters of the western Atlantic Ocean (Gutherz, 1967; Gutherz and Blackman, 1970; Topp and Hoff, 1972; Figueiredo and Menezes, 2000; 2003). Larvae of both species have been collected off Nova Scotia, Canada, but these were considered strays from more southern localities (Scott and Scott, 1988). These two species are morphologically similar and, although broadly sympatric in the western North Atlantic Ocean, are seldom taken together in the same collections. Their relatively small size (maximum to 55 mm standard length [SL] in *C. gymnorhinus* and 91 mm SL in *C. cornutus*), lack of commercial importance, infrequency of capture, and the probable low abundance of both species have resulted in their largely being ignored.

Published, detailed life history information for *C. cornutus* is sparse. Consequently, our knowledge of the biology, ecology, and geographic distribution of this species is limited to relatively few observations on maximum size (Parr, 1931; Longley and Hildebrand, 1941; Gutherz, 1967), size at maturity (Parr, 1931 [in part]; Longley and Hildebrand, 1941), reports of hermaphrodites (Gutherz, 1969), and general descriptions of geographic and bathymetric distributions (Parr, 1931 [in part]; Longley and Hildebrand, 1941; Gutherz, 1967; Topp and Hoff, 1972). *Citharichthys cornutus* is found from temperate regions of the North Atlantic Ocean off New Jersey (Goode, 1880; reported as *Citharichthys unicornis*, now considered a junior synonym of *C. cornutus*, see Norman, 1934; Fowler, 1952; Steves et al., 1999) and Hudson Submarine Canyon (Fahay, 2007) to subtropical waters off southern Brazil (Günther, 1880) and Uruguay (Figueiredo and Menezes, 2000; 2003). From the limited data, it appears that *C. cornutus* reaches sizes to about 89 mm SL (Gutherz, 1967), and although this species is known from depths ranging from 20 to 408 m (Gutherz, 1967; Topp and Hoff, 1972), it has been captured most frequently between 130 and 370 m (Gutherz, 1967).

Most published sources commonly cited for distributional information on *C. cornutus* are inaccurate. Data in Gutherz (1967) are the basis for the geographic range most frequently reported for adult *C. cornutus* (Robins and Ray, 1986; Munroe, 2003; McEachran and Fechhelm, 2005). Gutherz (1967) described the range as the continental shelf from off Georgia throughout warm-temperate and tropical regions of the western Atlantic to Brazil. Several earlier reports (Goode, 1880; Goode and Bean, 1895; Fowler, 1952), however, had already documented occurrences of *C. cornutus* (as *C. unicornis*) from more northern localities including those as far north as the outer continental shelf off New Jersey (see also Fahay, 2007). These earlier reports of *C. unicornis* (=*C. cornutus*) from more northern locales were overlooked in most recent studies where information has been compiled for this species (with exception of Fahay, 2007).

More information is available on the life history and distribution of *C. gymnorhinus*, which reportedly reaches a maximum size of about 55 mm SL (Gutherz and Blackman, 1970; Topp and Hoff, 1972). *Citharichthys gymnorhinus* is one of the smallest species of the genus and is also among the smallest of flatfishes (Munroe, 2005). It is found on the mid- to outer continental shelf at depths of 35–201 m, but has been collected most frequently between 30 and 90 m (Gutherz and Blackman, 1970; Topp and Hoff, 1972; Walsh et al., 2006). *Citharichthys gymnorhinus* inhabits subtropical and tropical regions of the western North Atlantic Ocean (Gutherz and Blackman, 1970; Topp and Hoff, 1972) from North Carolina (Quattrini and Ross, 2006) to Guyana (Topp and Hoff, 1972).

Although not rare, *C. gymnorhinus* has been captured less frequently than *C. cornutus*, and seldom has it been taken in abundance, especially on the continental shelf off the eastern United States. No summaries of biological information exist for *C. gymnorhinus* found off the east coast of the United States, and information from this region is restricted to limited geographic and bathymetric data based on few specimens—the data appearing in tables and appendices of various reports (see below). Most biological and ecological data for this species, including observations on habitat, depth of occurrence, size, size at maturity, and geographical distribution, are based on 47 specimens collected from the Florida Keys to Guyana, and the majority of these specimens were taken on the west Florida shelf during cruises of the RV *Hourglass* (Topp and Hoff, 1972). Recent summaries of information on adult *C. gymnorhinus* are based almost entirely on data originally presented in Gutherz and Blackman (1970) and Topp and Hoff (1972) and indicate a northernmost geographical limit for adults, either as the Bahamas (Robins and Ray, 1986; McEachran and Fechhelm, 2005; Lyczkowski-Shultz and Bond, 2006), Florida (Fahay, 2007), the Florida Keys (Robins and Ray, 1986; McEachran and Fechhelm, 2005), or perhaps the continental shelf as far north as off North Carolina (Munroe, 2003). Assessment of distributional information in these recent reviews indicated that the northernmost limits in the geographic range reported for *C. gymnorhinus* were inaccurate. Earlier published records of adult *C. gymnorhinus* from waters north of the Florida Keys and Bahamas, including those from off Georgia (Tucker, 1982) and South Carolina (Wenner et al., 1979a), were overlooked in these recent summaries. Recently, Walsh et al. (2006) again collected juveniles and adults of this species off Georgia, and Quattrini and Ross (2006) reported catching adults on the continental shelf off North Carolina, thereby documenting the northernmost latitude known for adult *C. gymnorhinus*. Although the captures in Quattrini and Ross (2006) are the first published records for *C. gymnorhinus* as far north as North Carolina, our examination of museum lots uncovered a specimen taken off North Carolina during the first part of the 20th century (see below).

The objectives of this study are to update and augment biological and distributional information for these two diminutive flatfish species. Data were gleaned from three sources: 1) specimens in fish collections, including specimens for which some information may have already appeared in published and gray literature, and including some specimens that we re-identified; 2) specimens in fish collections not previously reported; and 3) from recently collected specimens of both species captured off the southeastern United States. Additional information from other specimens reported in the literature, although not examined by us but where identifications were deemed reliable, is also included in the data summaries. The cumulative contributions of information from the above sources allowed us to note obscure distributional records for both species and also to compile more accurate summaries of life history, and ecological and distributional information for these flatfishes. In summarizing such data, we were able to correct longstanding inaccuracies in the reported distributions of these species and to evaluate this new distributional information in relation to contemporary hypotheses regarding shifts in ranges of continental shelf fishes due to effects of climate change.

Materials and methods

This study was initiated with the collection of both *C. gymnorhinus* and *C. cornutus* from the continental shelf off North Carolina (Quattrini and Ross, 2006; Ross, unpubl. data). Recognizing that captures of both species off North Carolina represent significant contributions to our knowledge of the distribution and ecology of these species, we initiated a complete review of available information on these fishes. Pertinent literature was examined to identify and validate published records of both *C. gymnorhinus* and *C. cornutus* (including records for type specimens of *C. unicornis* Goode, a junior subjective synonym of *C. cornutus*; see Norman, 1934) from localities off the eastern United States and adjacent areas in the Bahamas and northeastern Caribbean Sea. Major fish collections likely to have holdings of these species from this region were also surveyed and specimens were examined (Appendices 1 and 2), or data were taken from internet databases where identifications were deemed reliable. Details for institutional fish collections

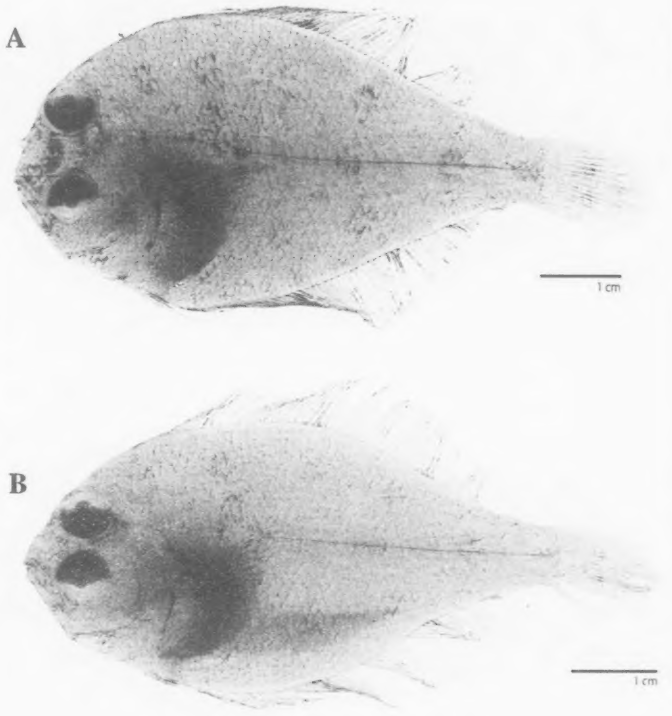

Figure 1

Adult *Citharichthys cornutus* from the western North Atlantic Ocean. (**A**) Male; North Carolina State Museum (NCSM) 47664; 65.1 mm standard length (SL); featuring secondary sexual dimorphisms in cephalic spination and wide interorbital space. (**B**) Female (NCSM 47664; 62.1 mm SL) with no cephalic spination and narrower interorbital space. Note also the elongate, pigmented ovary.

designated by acronyms in this study can be found at http://www.asih.org/codons.pdf. Additionally, specimens of both species were identified from materials collected during recent NMFS-Northeast Fishery Science Center (NEFSC) groundfish surveys, and data associated with these specimens were also included in this study.

All benthic specimens examined or noted through literature and museum searches were collected primarily by various types of bottom trawl, and a few specimens were also taken in benthic dredges. Descriptive geographic locations of collections taken on the continental shelf along the southeastern United States designated in Appendices 1 and 2 and elsewhere were based on their latitudinal positions in relation to terrestrial state boundaries, which may not necessarily coincide with the state boundaries on the continental shelf.

Fishes examined were identified, enumerated, and measured to the nearest mm SL, unless otherwise noted. Species were identified according to characters outlined in Gutherz and Blackman (1970). *Citharichthys cornutus* (Fig. 1, A and B) is distinguished from *C. gymnorhinus* (Fig. 2, A and B) in having scales on the snout (absent in *C. gymnorhinus*), 6 ocular-side pelvic fin rays (vs. 5), 40 or more lateral-line scales (vs. <40 scales in lateral line), and a dark spot in the axil of the ocular-side pectoral fin (vs. no dark spot in axil of pectoral fin). Male *C. cornutus* do not have large black spots in the middle of their dorsal and anal fins that are characteristic of male *C. gymnorhinus* (compare Figs. 1A and 2A), and male *C. cornutus* also have a much larger interorbital space compared with that of male *C. gymnorhinus*.

Sex and maturity of individuals were determined (where possible) by examining external sexually dimorphic characters and by macroscopic examination of gonads with light transmitted through the abdominal

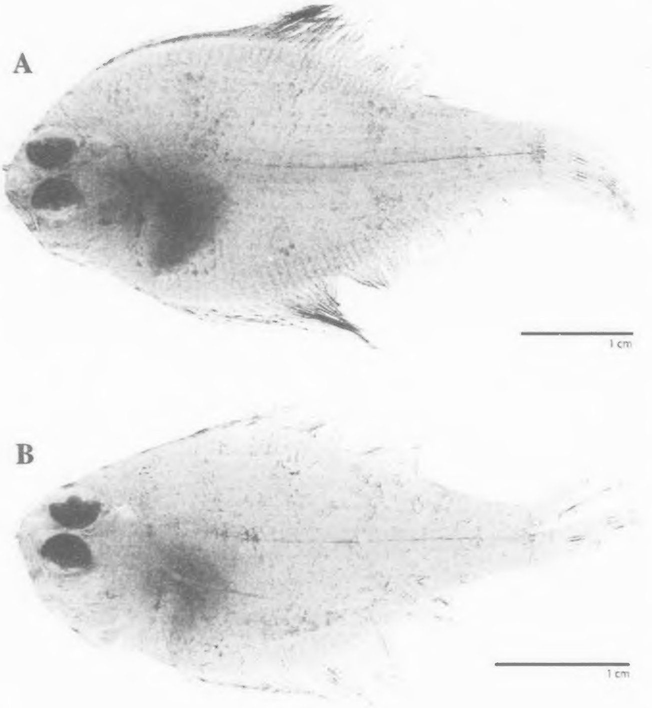

Figure 2

Adult *Citharichthys gymnorhinus* from the western North Atlantic Ocean. (**A**) Male; North Carolina State Museum (NCSM) 47657; 49.5 mm standard length (SL); featuring secondary sexual dimorphisms in cephalic spination, wider interorbital space and black blotches on dorsal and anal fins. (**B**) Female (NCSM 47662; 39.3 mm SL) lacking cephalic spination or black spots on dorsal and anal fins, and with narrower interorbital space. Note also the elongate, pigmented ovary.

region of the body. Adult *C. gymnorhinus* (Gutherz and Blackman, 1970; Topp and Hoff, 1972; this study) and *C. cornutus* (Parr, 1931; Gutherz and Blackman, 1970; this study) feature distinct sexual dimorphisms that facilitate macroscopic determination of sex of maturing and mature individuals of both sexes. Female *C. cornutus* lack dimorphic sexual features characteristic of male *C. cornutus* (compare Fig. 1, A and B), including the absence of rostral and cephalic spines, in having a much narrower interorbital space (usually <eye diameter), and females lack the dusky blind-side pigmentation observed in recently captured males (taken off North Carolina). Females also have a different size, shape, and extent of posterior elongation of the gonad compared with that of males. In mature females, the ovary is broadly triangular anteriorly, extends posteriorly for more than one-half the standard length of the specimen (see mature ovary in females in Figs. 1B and 2B), and is easily seen through the abdominal wall (vs. males with much smaller, rounded testes that do not undergo posterior elongation). For male *C. gymnorhinus* (Fig. 2A), secondary sexual characters include rostral and cephalic spination, conspicuous black blotches on dorsal and anal fins, dusky blind-side pigmentation (best observed in recently caught males), an elongate, fragile first fin ray (often broken) in the ocular-side pectoral fin, and small, rounded testes without posterior elongation. These features become conspicuous in some males between 29 and 35 mm SL and are well developed in all males ≥42 mm SL. In contrast, female *C. gymnorhinus* (Fig. 2B) lack cephalic spination, black pigmented blotches on dorsal and anal fins, and the dusky blind-side pigmentation characteristic of males. Also, with the onset of maturity, the ovaries undergo a conspicuous extensive posterior elongation (easily observed with light transmitted through the body), which,

as also occurs in *C. cornutus*, may extend for more than one-half of the standard length of the individual. Immature females of both species are identified by their shorter, more triangularly shaped ovaries that have either not yet begun to elongate, or that are only in the earliest stages of posterior elongation.

Results and discussion

Biological and ecological information from 594 *C. cornutus* (Appendix 1) and 214 *C. gymnorhinus* (Appendix 2) were included in this study. Of the 594 *C. cornutus*, size data were available for 566 individuals. Sizes were not available or were not taken for 28 of the *C. cornutus*; however, geographic and bathymetric data associated with these individuals were included in appropriate summaries. Size information was taken from 196 of the 214 *C. gymnorhinus* included in the study. One individual (a mature male) had a regenerated caudal region, and therefore it could not be measured accurately, and size data from this specimen were excluded. Depth of capture information was known for 578 of the 594 *C. cornutus* and for all 214 of the *C. gymnorhinus* included in the study.

Sex and maturity information was compiled from 430 of 566 *C. cornutus* that were measured. Sex could not be determined macroscopically for *C. cornutus* smaller than 20.0 mm. For 135 *C. cornutus*, although size information was available, no information was provided to determine the sex of these fishes. One specimen was damaged during collection and its sex could not be determined. Sex could not be determined for another individual of 68 mm because the gonad appeared to be undeveloped (macroscopic appearance was neither that of a typical testes or ovary) and although this individual is well within the size range for adults (see below), it does not feature any external sexually dimorphic characters typical of adult males, which also precluded macroscopic determination of its sex. Sex and maturity were determined for 190 of 214 *C. gymnorhinus*. We did not examine 25 *C. gymnorhinus*, including seven for which size data were available (8–38 mm); thus no information on their sex or maturity was available.

Citharichthys cornutus (Günther 1880)

Taxonomic note

Günther (1880) described *Rhomboidichthys cornutus* from specimens taken on the continental shelf in the western South Atlantic off Brazil. Later that year, Goode (1880) provided a description of *Citharichthys unicornis* based on three specimens (USNM 26003: 3 syntypes) collected on the outer continental shelf off southern New England (actually at a latitude off New Jersey; see Fowler, 1952). Norman (1934) first considered these two nominal species to be conspecific and this decision has been followed by subsequent authors, but the status of these nominal species is in need of further study. During the interim between Goode's (1880) description of *C. unicornis* and Norman's (1934) placement of this species in the synonymy of *C. cornutus*, several studies were published in which this species was listed or in which ecological, distributional, and systematic information was reported under the name *C. unicornis*. These earliest reports of *C. cornutus* from the western North Atlantic (Jordan and Gilbert, 1883; Günther, 1887; Jordan and Goss, 1889; Goode and Bean, 1895; Jordan and Evermann, 1898; Evermann and Marsh, 1902; Parr, 1931) were overlooked in nearly all contemporary compilations of information on the species, in part because *C. unicornis* Goode was not recognized as a junior synonym for *C. cornutus* (Günther).

The series of specimens reported in Goode and Bean (1895) comprises at least two species, including *C. unicornis* (=*cornutus*) and *C. gymnorhinus* (see below). Parr's study (1931) may also have contained a mixture of both species, but because he did not list any specific collection data for the 68 specimens from the USNM and MCZ identified as *C. unicornis* in his study, the possibility that two species were intermingled cannot be proven definitively. The majority of specimens of *C. unicornis* available to Parr from the USNM fish collection were those collected earlier during cruises of the RV *Albatross* and reported in Goode and Bean (1895). Several of these lots comprise mostly specimens of *C. gymnorhinus*; therefore, if these were the same specimens examined by Parr, it seems likely that his data set was compromised because it would have contained a mixture of at least two species.

Geographic distribution

Fifty-six different field collections (Appendix 1) containing juvenile and adult specimens of *C. cornutus* encompassed the geographic range from the outer continental shelf off New Jersey to the continental shelves off the northern coasts of the Bahamas, Cuba, Puerto Rico, and the Lesser Antilles (Fig. 3). All but five collections occurred south of 35°N latitude. Among collections examined were four from off New Jersey (we could not find specimens from the second location off NJ reported by Goode, 1880), seven from off North Carolina, 22 off South Carolina, three off Georgia, nine off Florida, five from the Bahamas, one off Cuba, two off Puerto Rico, and three others from the eastern Caribbean Sea. One early record (USNM 111520) purportedly of this species from off North Carolina was misidentified as *Citharichthys unicornis* (=*C. cornutus*) by Hildebrand (1941). This 56-mm total length (TL) male, taken on 13 September 1914, off Cape Lookout by the RV *Fish Hawk* at a depth of about 92 m (50 fm) is actually *C. gymnorhinus*, and the significance of this specimen is discussed under the account for that species.

Our knowledge concerning the geographic occurrence of *C. cornutus* in the western North Atlantic Ocean is now improved through the inclusion of previously published distributional data, by highlighting data for specimens previously listed only in published tables

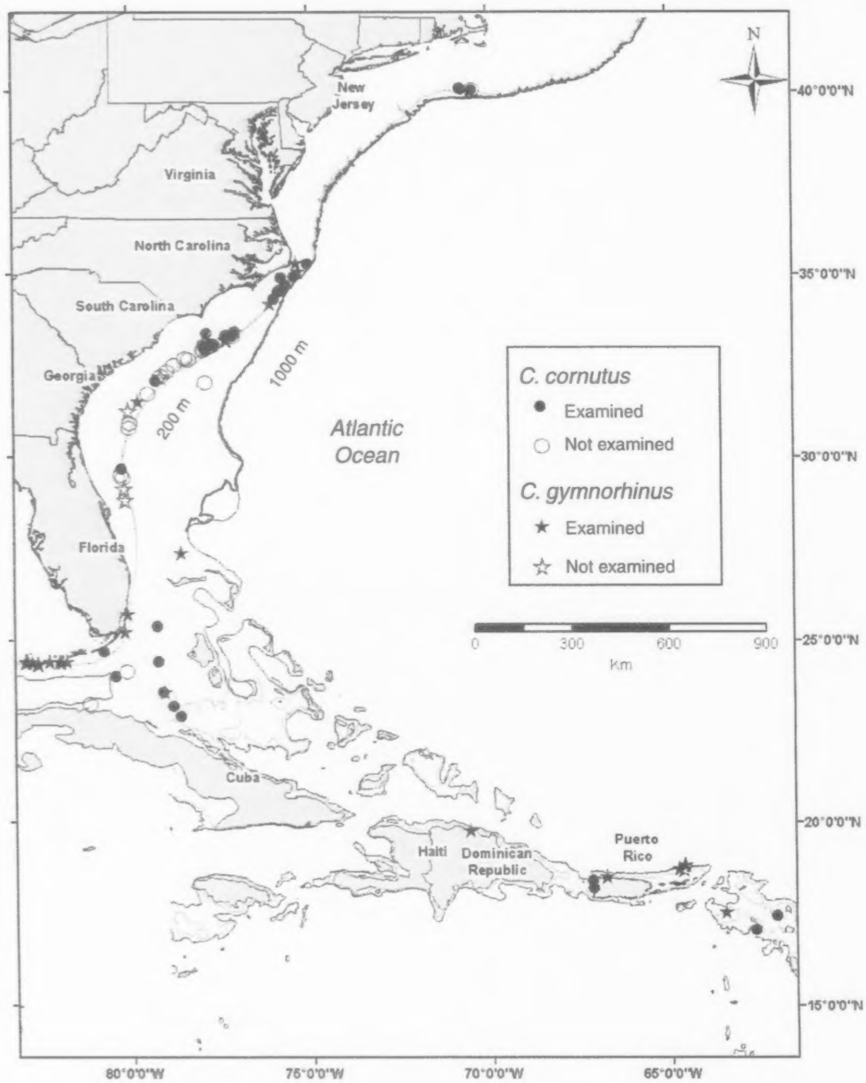
N
New Jersey
Virginia
North Carolina
South Carolina
Georgia
Florida
Cuba
Haiti
Dominican Republic
Puerto Rico
200 m
1000 m
Atlantic Ocean
C. cornutus
● Examined
○ Not examined
C. gymnorhinus
★ Examined
☆ Not examined
0 300 600 900
Km
40°0'0"N
35°0'0"N
30°0'0"N
25°0'0"N
20°0'0"N
15°0'0"N
80°0'0"W
75°0'0"W
70°0'0"W
65°0'0"W

Figure 3

Capture locations of specimens examined, or, of specimens cited in literature for which there are reliable identifications, for *Citharichthys cornutus* (n=594) and *C. gymnorhinus* (n=214). Points may indicate more than one fish and more than a single capture. Capture records for other specimens of *C. cornutus* from the Dry Tortugas Islands Region based on Longley and Hildebrand (1941) are not plotted because precise locality data were not provided for these specimens.

or appendices, and by inclusion of unpublished information associated with museum specimens and other uncatalogued specimens (Appendix 1). Based on these sources, the range of adult *C. cornutus* extends from the outer continental shelf off New Jersey (40°05.593′N, 70°42.75′W) and New York southward along the outer shelf of the eastern United States to Texas, and perhaps Yucatan, Mexico (Castro-Aguirre et al., 1999), the Bahamas, the Greater Antilles (Puerto Rico and Cuba), and Lesser Antilles (off Virgin Islands, St. Kitts Island), on the outer continental shelf throughout the Caribbean Sea, and off the Atlantic coast of South America to Uruguay. Larvae are known from Canadian Atlantic waters; several individuals have been collected at 41°33'N, 54°55'W (MCZ 77935) and 41°05'N, 66°31'W (Scott and Scott, 1988; Fahay, 2007).

The geographical distribution reported here is largely consistent with that known for the species as reported in Fahay (2007), but it is different from range information contained in literature accounts published during the last half of the 20th century. Goode (1880) first reported *C. cornutus* (as *C. unicornis*) from the western North Atlantic from two stations located on the outer continental shelf south of Rhode Island (40°02'54"N, 70°23'40"W and 40°02'36"N, 70°22'58"W). This capture site, actually off New Jersey (Fowler, 1952), is located on the shelf between the head of Alvin Submarine Canyon (40°00'N, 70°30'W) and a feature called "The Mud Patch" located just to the northwest of the canyon. The same distributional information for the species (deep waters of the Gulf Stream off Rhode Island) was reported by Jordan and Gilbert (1883) and Jordan and Goss (1889) from the data presented in the original description of the species by Goode (1880). Günther (1887) also listed this locality for *C. unicornis* on the basis of Goode's specimens. Fowler (1952) again listed *C. cornutus* among fishes of New Jersey on the basis of "offshore records" that most likely refer to specimens contained in Goode's (1880) original description of *C. unicornis*, because no other specimens were listed to indicate otherwise. In their treatise on deep-sea fishes, Goode and Bean (1895) again repeated the same distributional information for the syntypes of *C. unicornis* captured on the outer shelf off northern New Jersey, but they also provided data for additional specimens taken off South Carolina (33°18'N, 77°07'W) and in the Gulf of Mexico (28'36–38'N, 85°52–53'W). These new specimens increased the knowledge about the geographic distribution of this species along the southeast continental shelf of the United States. Although Goode and Bean also reported *C. unicornis* from the Straits of Florida off the Florida Keys (24°25'45"N, 81'46'W), re–examination of these specimens from *RV Albatross* station 2318 (USNM 45610; USNM 45677; USNM 143120) and RV *Albatross* station 2316 (USNM 129946) revealed they are not *C. cornutus*, but rather are *C. gymnorhinus* (see data summaries below for that species).

Scott and Scott (1988) considered their record of a larval *C. cornutus*, taken at 41°05'N, 66°31'W in 1982, to represent the northernmost point of the range of the species. They also considered that larvae of this species reported from the vicinity of the Canadian Atlantic are most likely strays from more southern locales. They missed earlier references documenting adults from the outer shelf region at 40°N and cited Georgia as the northern limit for the species following information in Tucker (1982). Other larval *C. cornutus* known from this general area (MCZ fish collection), including Georges Bank (Fahay, 2007), indicate the possibility that larvae caught in this region could also be produced by more localized spawning of *C. cornutus*. FishBase (Froese and Pauly, 2010; www.fishbase.org) also shows the western North Atlantic distribution of this species as Canada to Georgia based on the larva reported in Scott and Scott (1988).

Additional records of this species from off the southeastern coast of the United States and nearby areas include those in an unpublished dissertation by Staiger (1970), who detailed distribution of this species in the Straits of Florida region based on 143 specimens. He reported that *C. cornutus* occurs along the continental margin of the Straits from off the Dry Tortugas to Miami, also in the central Straits near the Cay Sal Bank, and along the insular margin of the Straits from the Santaren Channel to the Little Bahama Bank. Quattrini and Ross (2006) caught this species on the continental shelf off North Carolina but provided no further comments on the distribution of the species (because their specimens are included in the present study). Eight specimens of *C. cornutus* have also been taken at two locations off Puerto Rico (Evermann and Marsh, 1902; this study) and off the northern coast of Cuba near Provincia de Matanzas (Vergara Rodriguez, 1974). Cervigón (1996) recorded the species from off Venezuela but indicated that it is poorly documented from this area.

Other studies published during the last century contained more general, and often vague, information or commentary on the distribution of this species. For example, Jordan and Evermann (1898) listed it as occurring in deep waters of the Gulf Stream. Parr (1931) did not report any specific capture information for the approximately 68 specimens (largest series examined to that date) in his study. Instead, he mentioned that although very little was known about the distribution of *C. cornutus*, it was generally regarded as occurring in deep waters of the Gulf Stream. Norman (1934) considered *C. cornutus* to have a disjunct distribution with a northern range in deep waters of the Gulf Stream and a southern distribution off the coast of Brazil. Longley and Hildebrand (1941) reported the species as occurring in the Gulf Stream from the Dry Tortugas to at least off the southeast coast of New England (presumably from earlier literature records off New Jersey). Topp and Hoff (1972) listed this as a deepwater species in the Gulf of Mexico. Lyczkowski-Shultz and Bond (2006) described the range of *C. cornutus* as the Atlantic and Gulf coasts of the United States, without specifying any geographic limits. In a summary of distributional information for *C. cornutus*, Gutherz (1967) reported that its geographic range included the outer continental shelf along the Atlantic and Gulf coasts of the United States from Georgia to Texas, the Bahamas, the Greater Antilles, off Yucatan, Mexico, throughout the Caribbean, and off the Atlantic coast of South America to Brazil. Although Gutherz (1967) adequately summarized capture locations for the species in the middle portions (extreme southeastern United States, Gulf of Mexico, and Caribbean Sea) of its geographic range, he did not mention previous captures of the species from north of Georgia.

Beginning with Gutherz (1967), captures of adult *C. cornutus* from off New Jersey (Goode, 1880; and cited in other studies) and South Carolina (Goode and Bean, 1895; Wenner et al., 1979a; 1979c; 1979d; 1980) were overlooked in nearly all subsequent contemporary literature, and misinformation regarding the northern limits of distribution for *C. cornutus* was perpetuated. For example, Hoese and Moore (1977) reported the distribution of *C. cornutus* as the northwestern Gulf of Mexico, and from Georgia throughout the Caribbean to Brazil, later (Hoese and Moore, 1998) adding the Bahamas to this distribution. Tucker (1982: Table 1) also listed the geographic range for adults as Georgia to Brazil (although he illustrated in a map that larvae were known from areas north of Georgia at about Cape Fear, NC). Robins and Ray (1986) and Boschung (1992) repeated the same distributional information for the northern point of the geographic range (Georgia) for *C. cornutus* as that appearing in Gutherz (1967). Cervigón (1996) listed the geographic distribution as the eastern United States, Bahamas, and northern Gulf of Mexico to Brazil. Castro-Aguirre et al. (1999) tentatively listed the species from the Veracruz, Mexico, region on the basis of a study by Lozano-Vilano et al. (1993), and reported the geographic distribution of the species from Georgia, Florida, and Gulf of Mexico to Brazil, including the Bahamas and Antilles. Figueiredo and Menezes (2000; 2003) also listed the northern limit of the geographic range of *C. cornutus* as Georgia, as did Saavedra-Díaz et al. (2000). Munroe (2003) reported the distribution as the continental shelf off the Atlantic and Gulf coasts of the United States from North Carolina to Texas, which distribution is essentially the same as that given in McEachran and Fechhelm (2005). Historical captures of *C. cornutus* from off New Jersey were also overlooked (J. A. Moore and K. E. Hartel, personal commun.[1]) by Moore et al. (2003) and Hartel et al. (2008) in checklists of the deepwater (≥200 m) resident fishes from the Mid-Atlantic Bight area south of New England.

Among contemporary literature, only Fahay (2007) has provided a more accurate assessment of the northernmost occurrences of *C. cornutus*. Although he notes that the geographic range usually reported in the literature is from Georgia to Brazil, including the Gulf of Mexico and Caribbean Sea, he also has observed that adults are fairly common as far north as Cape Hatteras and Hudson Canyon and that larvae are collected as far north as Georges Bank. A recent capture of one specimen of *C. cornutus* from off New York is reported by Steves et al. (1999: their Table 3) and a photograph provided by M. Fahay (personal commun.[2]) indicates that at least five other specimens were taken recently on the continental shelf off New Jersey.

Bathymetric distribution

Overall, the 578 specimens for which information on depth of capture was available were captured at depths ranging from 68 to 287 m (Appendix 1). The majority of specimens (496 of 578=85%) were taken between 101–200 m (Fig. 4A). Only 31 (5.3%) *C. cornutus* in this study were taken shallower than 100 m, and only 61 (10.5%) specimens were collected deeper than 200 m (Fig. 4A).

Specimens examined in this study were collected within the bathymetric range generally reported for this species; however, our specimens did not represent the depth extremes reported for this species. This species is usually reported from outer shelf depths where these fishes are associated with soft bottoms, including sand-mud substrata (Staiger, 1970; McEachran and Fechhelm, 2005; Fahay, 2007). For example, Goode and Bean (1895) reported that their specimens were taken between about 83 and 285 m; however, their study included both *C. cornutus* and *C. gymnorhinus*. The depth range for specimens of *C. cornutus* in Goode and Bean is actually 174–285 m. Off the Dry Tortugas, Longley and Hildebrand (1941) reported the distribution of *C. cornutus* as benthic habitats in the Gulf Stream at depths of about 81 to somewhat less than 185 m, and that abundance was highest near 120 m. Staiger (1970) reported a depth range for the species in the Florida Straits region from 83 to 260 m. Gutherz (1967) listed the depth range for *C. cornutus* throughout its geographic range as 27–366 m and that captures generally exceeded 137 m; this range was repeated in several publications (Tucker, 1982; McEachran and Fechhelm, 2005; and Fahay, 2007). Topp and Hoff (1972) reported that off West Florida this species is known from the outer shelf or shelf edge; those in the Gulf of Mexico can be found at depths exceeding 350 m (5 out of 38 of their specimens were collected at these depths), and in the Caribbean it is usually found deeper than 137 m. Boschung (1992) listed the depth range for *C. cornutus* off Alabama as 24–172 m. Robins and Ray (1986) indicated a depth range of 30–400 m, usually deeper than 140 m for the species. Cervigón (1996) reported that this species inhabits depths between 30 and 400 m, but generally less than 300 m. Hoese and Moore (1977; 1998) considered this to be a deepwater species ranging from about 28–368 m, generally >138 m. Saavedra-Díaz et al. (2000) reported a depth range of 24–400 m. Munroe (2003) and Lyczkowski-Shultz and Bond (2006) reported this species at depths of 20–370 m, but generally deeper than 130 m. Off southern Brazil, Figueiredo and Menezes (2000) noted that *C. cornutus* is captured in fisheries conducted at depths of 20–192 m, and a maximum depth record of 365 m has been documented for this species in this region.

Size

Our specimens ranged in size from 17.2 to 81.3 mm SL (Fig. 5A). Overall, approximately 48% (272 of 566) of

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[1] Moore, Jon A., and Karsten E. Hartel. 2008. Honors College, Florida Atlantic University, Jupiter, FL 33458 and Museum of Comparative Zoology, Harvard Univ., 26 Oxford Street, Cambridge, MA 02138.

[2] Fahay, Michael. 2006. (Retired.) James J. Howard Marine Sciences Laboratory at Sandy Hook, Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 74 Magruder Road, Highlands, NJ 07732.

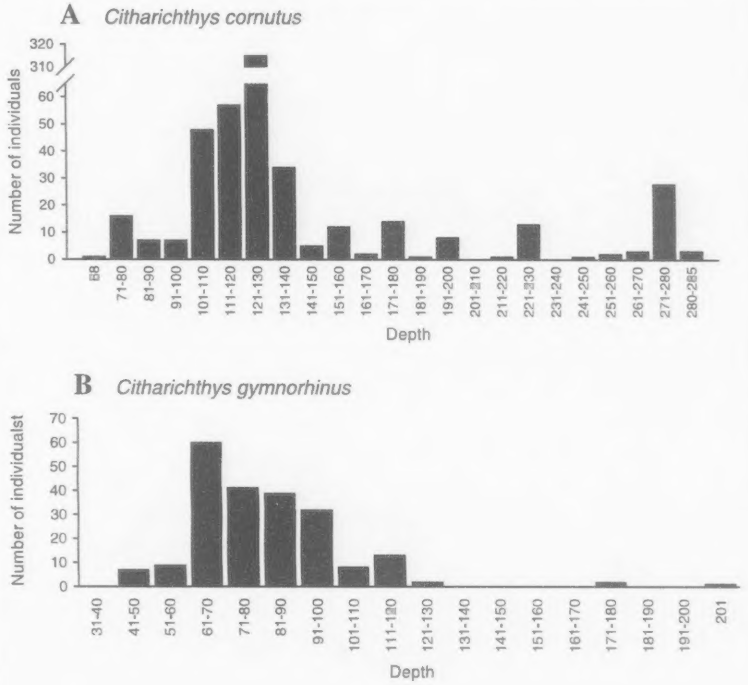

Figure 4

Mean depth of capture (at 10-m intervals) for two species of *Citharichthys* captured off the east coast of the United States and nearby regions. (**A**) *Citharichthys cornutus* (n=578). (**B**) *Citharichthys gymnorhinus* (*n*=214).

the specimens measured 60 mm or larger; but only 27 (4.7%) exceeded 70 mm. Males (259 of 430, ca. 60% of total fish for which sex was determined) ranged in size from 20.2 to 79.1 mm (Fig. 6A). Females (171 of 430=ca. 40% of total fish for which sex was determined) attained similar sizes (28.0–81.3 mm) to those recorded for males (Fig. 6B). Despite attaining nearly the same maximum size, males overall were usually larger than females and slightly more than twice as many males (169 or 39.3% of 430 fish for which sex was determined) reached 60 mm or larger than did females (48 or 11% of total fish for which sex was determined).

Size distributions in our samples are similar to those recorded for the species in other studies, but are slightly smaller than the maximum size (about 91 mm SL) reported for the species (Longley and Hildebrand, 1941; Gutherz, 1967; Cervigón, 1996). From a size range of 32–68 mm SL (*n*=68), Parr (1931) concluded that *C. cornutus* is a small species reaching only about 70 mm SL. But, as noted above, his results were likely based on a mixture of both *C. cornutus* and *C. gymnorhinus*. Norman (1934) reported sizes of 47–87 mm SL for six males, and 58 mm SL for one female. For *C. cornutus* collected off the Dry Tortugas, the largest size obtained by Longley and Hildebrand (1941) was slightly larger than 90 mm (TL?). Gutherz (1967) illustrated a male measuring 89 mm SL, but later (Gutherz, 1969), reported a maximum length for *C. cornutus* of only about 75 mm SL. Staiger (1970:64) examined 85 males and 35 females from the Straits of Florida that ranged in size between 26 and 70 mm SL. Topp and Hoff (1972) measured 38 specimens between 47.5 and 74.1 mm SL. Cervigón (1996) listed a maximum size of 91 mm SL for the species. Saavedra-Díaz et al. (2000) reported sizes for seven specimens taken off Colombia ranging from 46.7 to 61.8 mm SL. In other studies (Robins and Ray, 1986; Munroe, 2003; McEachran and Fechhelm, 2005), a maximum size of 100 mm TL was recorded (apparently rounded upward on the basis of other literature).

Size at maturity

Sex was determined for 430 of the 566 (ca. 76%) individuals measured. Among males (Fig. 6A), 32 of 259 (about 12%), ranging from 20.0 to 71.4 mm, are immature; whereas, 227 (87%), measuring 36.5–79.1 mm, are mature. All nine males $\leq$ 35.0 mm are immature, and 3 of 4 males between 35 and 40 mm are also immature.

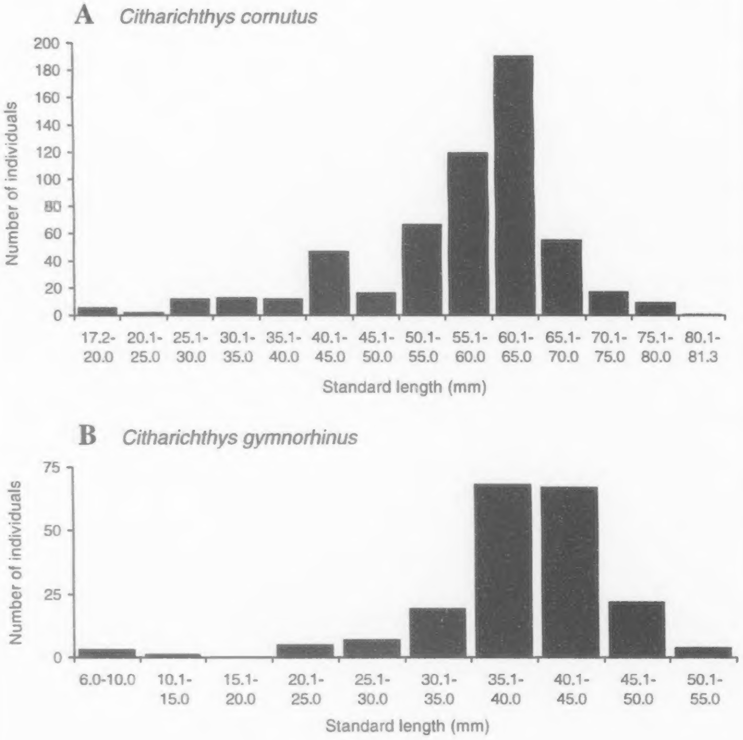

Figure 5

Size distribution (standard length) for two species of *Citharichthys* captured off the east coast of the United States and nearby regions. (**A**) *Citharichthys cornutus* (n=566). (**B**) *Citharichthys gymnorhinus* (n=196).

Between 40 and 45 mm, 7 of 10 males are mature, but in the next size category (45–50 mm) only 4 of 9 males are mature. Between 50 and 55 mm, 90% of the males are mature, and between 55 and 65 mm, 95–98% of the males (42 of 44 and 126 of 129, respectively) are mature. Nearly all males (n=38 of 40) ≥65.1 mm are mature.

Among the 171 females examined (Fig. 6B), 18 (28.0–55.1 mm) are immature, whereas mature females (n=153) range in size between 41.5 and 81.3 mm. Among the smallest females, 14 of 15 (93%) ranging between 28.0 and 45.0 mm are immature. Between 45.1 and 50.0 mm, only 1 of 3 females are immature, and among females ≥50 mm, only three (51.1, 51.8, and 55.1 mm) are immature. Of mature females, 2 of 3 females between 45.1 and 50.0 mm are mature, whereas between 50.1 and 55.0 mm about 93% (28 of 30) of the females are mature, and all but one female ≥ 55.1 mm are mature.

The largest collection of *C. cornutus* from off the eastern seaboard of the United States (NCSM 47664) contains 314 fish ranging in size from 20.0 to 68.0 mm. The sample comprises 177 males (20–68 mm), 136 females (28–64 mm), and 1 individual (68 mm) of unknown sex. The sex ratio for this sample is 1.3:1.0 males to females. Among males, 164 are mature (48–68 mm), and 13 others (20–49 mm) are immature. Most of the 136 females (n=121, 47–64 mm) are mature and only 15 (28–46 mm) are immature. Co-occurrence of juveniles and adult males and females in the same collection indicates that both sexes and both life stages occupy similar depths and probably occur in the same microhabitat(s).

Before this study, little information was available regarding size at maturity for *C. cornutus*. Earlier literature on *C. cornutus* emphasized the sexual dimorphisms exhibited by this species and the relative sizes when these dimorphic features become evident. Parr (1931:17) provided the most detailed account on size, morphological features, and striking sexual dimorphism exhibited in this species (as *C. unicornis*) based on at least 37 males and 31 females ranging from 32 to 68 mm SL (note again that his specimens may have been a mixture of *C. cornutus* and *C. gymnorhinus*). Norman

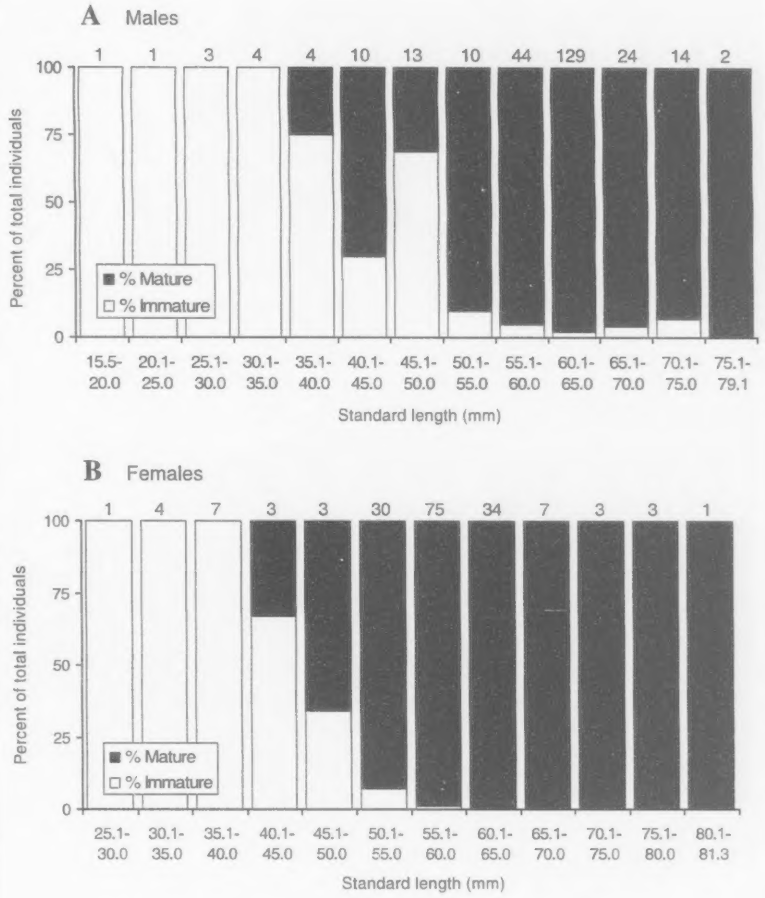

Figure 6

Size (standard length) and maturity information for 430 *Citharichthys cornutus* captured off the east coast of the United States and nearby regions. (**A**) Males (n=259). (**B**) Females (*n*=171). Number above each column is the number of individuals examined in that size range.

(1934:153) examined seven specimens of *C. cornutus* (including types of *Rhomboidichthys cornutus* and several USNM specimens), noted sexual dimorphisms of this species, and also commented that a more complete description of these dimorphic differences was available in Parr (1931). Longley and Hildebrand (1941:43) provided descriptive information on sexual dimorphism, as did Gutherz (1969), who also reported the capture of two adult hermaphroditic specimens from off Nicaragua. Longley and Hildebrand (1941) further commented that the sexes were easily distinguished at sizes of 55 mm (TL?) and greater because the posterior elongation of the ovaries was easily observed through the body wall of females. We also found that all females but one taken off the east coast of the United States that are ≥55 mm are sexually mature.

Abundance

Overall, the majority of specimens examined were taken on the outer continental shelf of the South Atlantic Bight. Ten different collections of *C. cornutus* from this region contained solitary individuals (Appendix 1), and another nine collections contained two or three specimens. The largest collections of *C. cornutus* from the east coast of the United States are all from North Carolina and southwards, including one collection off North Carolina with 12 specimens, seven off South Carolina (two with

12, one each with 15, 24, 26, and 30 individuals), and the single largest collection (314 individuals) of *C. cornutus* from this region (NCSM 47664) from off South Carolina (at 33°25.389'N, 77°02.234'W). Other notable collections are those of 16 specimens from the Dry Tortugas region, and another collection containing 24 specimens (USNM 282789) made off the Bahamas.

Citharichthys cornutus is found in relatively high densities in the Dry Tortugas region (Longley and Hildebrand, 1941). Although it is unclear how many specimens they encountered, Longley and Hildebrand (1941:43) noted that *C. cornutus* was "rather common" in this area, with sometimes 50 or more individuals taken together. Other significant collections of *C. cornutus* from the eastern Gulf of Mexico containing 43, 47, 63, 100, 103, 172, and 321 specimens are curated in the AMNH fish collection (see *Additional material* section).

Citharichthys gymnorhinus

Geographic distribution

We identified 214 juvenile and adult *C. gymnorhinus* in a total of 42 different field collections from the continental shelf off North Carolina to the Dominican Republic, Virgin Islands, and Puerto Rico (Fig. 3; Appendix 2). Of collections containing *C. gymnorhinus*, five are from the shelf off North Carolina, including the northernmost capture of the species made off Cape Hatteras (35°05.51'N). Nine were made on the continental shelf off South Carolina, and at least two collections were made off Georgia. Most (n=17) collections of *C. gymnorhinus* are from the continental shelf off Florida, including the Straits of Florida and the Dry Tortugas regions. *Citharichthys gymnorhinus* not only was less frequently captured at insular regions in the eastern Caribbean Sea than off the southeastern United States, but it is also known from relatively few specimens per collection at these Caribbean locations (e.g., five collections from Virgin Islands yielded only 21 specimens). Only two collections (n=3 specimens) from off the Bahamas were found, and we note single captures of this species from off the northern coasts of Puerto Rico and the Dominican Republic.

The northernmost records for juvenile and adult *C. gymnorhinus* are those from the continental shelf just south of Cape Hatteras, NC (NMFS Survey specimens; NCSM records; Quattrini and Ross, 2006). Larval *C. gymnorhinus* have been collected from sites much farther north than those reported for adults. For example, Scott and Scott (1988) reported that a 13-mm larva of *C. gymnorhinus*, collected in 1982 at 41°21'N, 66°14'W, represented the first record for this species from Canadian waters and also was the northernmost record of occurrence for the species. Other captures of larval *C. gymnorhinus* from this general region include at least three lots (one taken at 41°35'28"N, 66°24'75"W: the others at 33°24'07"N and 32°58'37"N) curated in the Atlantic Reference Center (ARC) fish collection and one lot curated in the MCZ collection (MCZ 77935) taken at 41°33'N, 54°55'W. Scott and Scott (1988) considered that larval *C. gymnorhinus* occurring in Canadian waters were strays from more southern locations. Museum records at ARC and MCZ document captures of larval *C. gymnorhinus* at or just beyond 41'N latitude over the course of several years, indicating that larval *C. gymnorhinus* at this latitude may be found more frequently than previously recognized. The record of *C. gymnorhinus* from off New Jersey (Able, 1992) is also based on larvae. Absence of adults in areas north of North Carolina may indicate that suitable habitat or appropriate environmental conditions are not available for juvenile settlement or for adult survival in these areas.

Earlier occurrences of larval *C. gymnorhinus* in the South Atlantic Bight were detailed by Tucker (1982), who reported the northern range for larval *C. gymnorhinus* at about Cape Fear, NC. More recently, Powell et al. (2000) and Grothues et al. (2002) also listed this species among the larval fish assemblages off Cape Hatteras, NC, and Fahay (2007) reported collecting larvae in the area north of Cape Hatteras from January to November, with peak occurrence from August through September. Powell et al. (2000) considered that larval *C. gymnorhinus* in Onslow Bay, NC, were most likely produced either by adults spawning in outer-shelf waters (55–185 m) nearby or were larvae produced by fishes spawning south of their study area. Off Georgia, *C. gymnorhinus* is only a minor component of the larval fish assemblage in these waters (Marancik et al., 2005).

Before the work of Quattrini and Ross (2006), studies of fishes off North Carolina did not list adult or juvenile *C. gymnorhinus* among species occurring there. Although specimens cited in Quattrini and Ross (2006) represent the first published record of adult *C. gymnorhinus* taken on the continental shelf off North Carolina, these are not the first specimens known from the area. Examination of catalogued museum lots and uncatalogued specimens from NMFS-NEFSC groundfish surveys (USNM uncat., see Appendix 2) reveals that other specimens had been captured off North Carolina before the Quattrini and Ross (2006) study. The earliest collection of *C. gymnorhinus* from off North Carolina that we can document is that of a 45.4-mm male (USNM 111520) taken 13 September 1914, off Cape Lookout by the RV *Fish Hawk*, at a depth of about 92 m. Collection of this specimen pre-dates recognition and formal description of the species by Gutherz and Blackman (1970). Originally, Hildebrand (1941) misidentified this specimen as *Citharichthys unicornis* (=*C. cornutus*; see Norman, 1934); however, meristic features and color pattern, including dark pigment blotches on its dorsal and anal fins, reveal that it is an adult (45.4 mm SL) male *C. gymnorhinus*.

One of the earliest reports of this species off South Carolina is that of Wenner et al. (1979a), who recorded a single specimen of *C. gymnorhinus* taken at 86 m during the 1973 fall trawl survey. Other specimens taken off South Carolina during the 1970s are curated in several fish collections (AMNH, GMBL, UF; see Appendix 2). In his article describing larval development of *C. gymnorhinus*, Tucker (1982) described the northern limit for adult *C. gymnorhinus* as off Georgia (however, his Table 1 noted the geographic range as Florida to Guyana). More recently, Walsh et al. (2006) have collected five small specimens of this species between 35 and 48 m on the inner continental shelf off Georgia. Gutherz and Blackman (1970) documented occurrence, based on 34 specimens, of *C. gymnorhinus* off the Florida Keys, the Antilles, off northern and western Bahamas, northern Hispaniola, northern Puerto Rico, Tobago, and the Caribbean Sea off Colombia, Panama, and Nicaragua. An additional record of *C. gymnorhinus* (as an undescribed *Citharichthys* species) was included by Starck (1968) from off Alligator Reef, Florida. Topp and Hoff (1972) recorded the species from several additional locations, including the continental shelf off west Florida, and also at sites off northern Cuba, the Virgin Islands, Venezuela, and Guyana. Boschung (1992) listed the geographic range as the northern Gulf of Mexico, and Bahamas to the western Caribbean and northern South America.

Recent literature and an on-line database synthesizing information on *C. gymnorhinus* have perpetuated misinformation concerning the northern limits of distribution for this species. Robins and Ray (1986), Cervigón (1996), Saavedra-Díaz et al. (2000), Munroe (2003), McEachran and Fechhelm (2005), Lyczkowski-Shultz and Bond (2006), Fahay (2007), and Froese and Pauly (2010) indicate a northernmost geographical limit for adult *C. gymnorhinus* as the Bahamas or the Florida Keys, which is essentially the same distribution reported in Gutherz and Blackman (1970) and Topp and Hoff (1972). Earlier records of adult *C. gymnorhinus* north of the Florida Keys and the Bahamas published after studies by Gutherz and Blackman (1970) and Topp and Hoff (1972) were overlooked owing to a lack of thorough investigation. Perhaps these oversights resulted because citations of *C. gymnorhinus* from this area are infrequent and scattered among species lists that are included only in tables or appendices of regional studies (e.g., Wenner et al., 1979a; 1979b; 1979c; 1980) or because some records are not vouchered by specimens and are difficult to verify. For other studies (i.e., Tucker, 1982), conflicting information reported within the same work regarding the distribution of this species is confusing.

Bathymetric distribution

Citharichthys gymnorhinus examined in the present study were collected over a depth range from 35 to 201 m (Appendix 2; Fig. 4B). Approximately 90% (193 of 214) of these fish were taken at depths averaging 61–120 m. Only 16 individuals were captured shallower than 60 m, with the shallowest depths recorded (Walsh et al., 2006) for five individuals taken between 35 and 48 m off Georgia (specimens not examined by us).

Capture locations for 48 *C. gymnorhinus* collected at depths averaging 100 m or more occurred in a variety of areas including those off North Carolina and South Carolina, in the Straits of Florida, and at the Bahamas. Only five individuals (2.3% of the total) examined in the present study were collected at depths averaging deeper than 120 m, and except for single specimens of *C. gymnorhinus* taken at 130 m and 123–127 m off North Carolina and South Carolina, respectively, the other three specimens were taken at insular locations off the Bahamas (two between 166–193 and one at 201 m). In fact, of examined specimens taken at insular locations in this region (n=26), all but five were collected at or beyond 70 m, and usually much deeper (Appendix 2).

The depth range summarized in the present study is similar to that reported previously for this species. For example, Gutherz and Blackman (1970) noted captures of *C. gymnorhinus* in depths of 37–92 m, and one specimen (USNM 203602), their deepest, was collected from about 201 m off the Bahamas (27°23′N, 78°35′W) (this specimen also represents our deepest record). Topp and Hoff (1972) reported that off west Florida this species is found at moderate depths on the continental shelf; 23 of 35 of their specimens were found at their deepest station (73 m), and all of their specimens were found deeper than 55 m. Tucker (1982: Table 1) listed a depth range of 37–201 m for adult *C. gymnorhinus* based on data from Gutherz and Blackman (1970). Saavedra-Díaz et al. (2000) reported that this species is found between 20 and 40 m in Colombian waters and between 37 and 139 m elsewhere. In nearly all other recent studies where information has been compiled for this species (Robins and Ray, 1986; Cervigón, 1996; Munroe, 2003; McEachran and Fechhelm, 2005; Lyczkowski-Shultz and Bond, 2006; Fahay, 2007), *C. gymnorhinus* are reported to be found on the continental shelf to depths of 200 m but more commonly taken in the shallower portion of this depth range (usually between 30 and 90 m).

Size

The largest *C. gymnorhinus* measured in this study are males of 52.4 and 52.1 mm (Fig. 7A), which is close to the reported maximum size (about 55 mm SL) observed for the species. A total of 131 males ranged from 20.3 to 52.4 mm (Fig. 7A), whereas females (n=58) were 26.2–48.0 mm (Fig. 7B). Most males (122 of 131, 93%) were 30–50 mm, and only four were larger than 50 mm. For females, most (42 of 58, 74%) were 35–45 mm, and only one (48.0 mm) exceeded 45 mm.

The size ranges for *C. gymnorhinus* taken along the eastern United States and nearby regions are comparable to those reported for this species from other parts of its geographic range. For example, Gutherz and Blackman (1970), who reported that *C. gymnorhinus* is the smallest species of *Citharichthys*, stated that maximum size for specimens they examined did not exceed 60 mm SL, when actually the largest of 34 specimens measured in their study (male, 52.5 mm SL) was smaller than this stated maximum size. Ten males examined in their study ranged in size from 41.9 to 52.5 mm SL, whereas four females were 32.9–41.8 mm SL. The largest of 47 individuals examined by Topp and Hoff (1972) was a

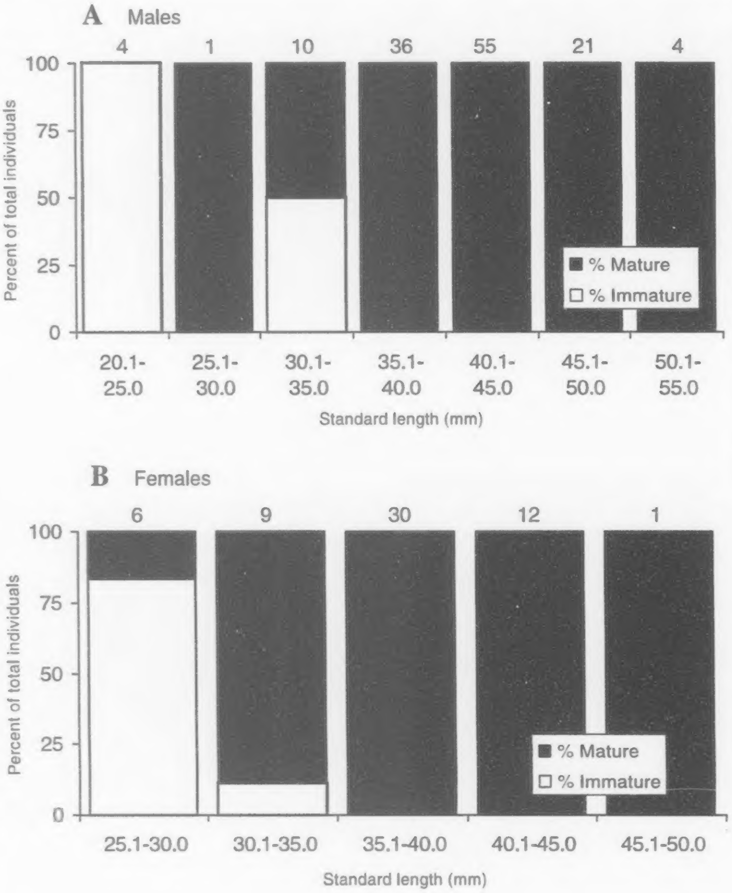

Figure 7

Size (standard length) and maturity information for 189 *Citharichthys gymnorhinus* captured off the east coast of the United States and nearby regions. (**A**) Males (n=131). (**B**) Females (*n*=58). Number above each column equals the number of individuals examined in that size range.

male of 53.7 mm SL, and they indicated a maximum size for *C. gymnorhinus* of less than 55 mm SL. Topp and Hoff (1972) did not provide a complete size breakdown for all specimens they examined but did give size ranges for these specimens. Males (*n*=25) ranged in size from 24.9 to 53.7 mm SL; females (*n*=6) were 36.1–47.0 mm SL. Cervigón (1996) reported that 55 mm SL was the maximum size observed for *C. gymnorhinus* taken off Venezuela. Fahay (2007) also considered *C. gymnorhinus* to be a dwarf species that seldom exceeds 55 mm SL in length.

Other literature reporting sizes for *C. gymnorhinus* larger than the maximum size observed in our study and the studies listed immediately above based their maximum sizes on an estimated value of 60 mm SL following that listed in Gutherz and Blackman (1970). These reports include those of Munroe (2003), McEachran and Fechhelm (2005), Robins and Ray (1986), and also FishBase (Froese and Pauly, 2010), which report a maximum size for *C. gymnorhinus* of 75 mm TL. This estimate of total length, corresponding to approximately 60 mm SL, is an overestimate of actual observations of maximum sizes recorded for the species from throughout its range.

Size at maturity

In other literature (where sizes of *C. gymnorhinus* are larger than the maximum size observed in our study and in the studies listed immediately above), maximum length was estimated at 60 mm SL as listed in Gutherz and Blackman (1970). Of 131 males examined in the present study, all but nine are mature with obvious discernible dimorphic characters typical of sexually mature individuals (Fig. 2A; and discussed above). All four males ≤25.0 mm are immature. The only male (29.0 mm) in the next larger size class is the smallest mature male in the study (Fig. 7A). Between 30 and 35 mm, half (5 of 10) of the males examined are immature, whereas five others are mature and display external features characteristic of adult males. At 35.1 mm and larger, all males examined are mature. Of 58 female *C. gymnorhinus* examined, all but six (26.2, 26.5, 27.5, 27.6, 28.0, and 30.1 mm) are mature (Fig. 7B). The smallest mature female was 30 mm, and eight others smaller than 35 mm are also mature. At sizes ≥35.1 mm SL, all females are mature.

No published information on maturity schedules or size at maturity based on microscopic staging of gonads is available for *C. gymnorhinus*. Information on size at maturity for this species is based only on examination of external sexual dimorphisms for males and external examination of ovaries of females. For example, Gutherz and Blackman (1970) noted that the smallest mature male in their study was 42 mm SL. Small size at maturity compared to that of congeners was also noted for *C. gymnorhinus* in specimens taken in the eastern Gulf of Mexico off the west Florida shelf (Topp and Hoff, 1972). Among the six females examined by Topp and Hoff, ovaries of a 21.0-mm-SL female were maturing (observed macroscopically), whereas ovaries of a 30.2-mm-SL female were filled with ripe, spherical eggs. They also observed that males of the same size had sexually dimorphic features, indicating they were mature at sizes similar to those at which females reach maturity.

Abundance

Of 42 field collections containing *C. gymnorhinus* (Appendix 2), 16 comprised solitary specimens, 11 consisted of two or three specimens each, and 15 collections contained four or more specimens. The largest collections of *C. gymnorhinus* comprised 36 and 23 specimens taken in the Straits of Florida off Key West and off South Carolina, respectively. Other significant collections of this species are those containing 19, 16, and 15 specimens taken in single trawls in the Straits of Florida, off the eastern side of the Florida Peninsula, and South Carolina, respectively. Three other trawls made off North Carolina, South Carolina, and the British Virgin Islands contained eight, nine, and eight individuals, respectively.

From the collections we examined and those listed in previous studies that provide detailed information on *C. gymnorhinus* (Gutherz and Blackman, 1970; Topp and Hoff, 1972), we believe that this species apparently is not taken anywhere in its geographic range in such large numbers as is *C. cornutus* (see above). The largest collections reported in Gutherz and Blackman (1970) and Topp and Hoff (1972) contained only 10 and 11 individuals, respectively, for trawl catches made in the Straits of Florida and off Venezuela, but most of their collections of *C. gymnorhinus* contained only five or fewer specimens. Wenner et al. (1979b; 1979c) listed collections of 15 and 12 specimens taken off the east coast of Florida (28°50.3′N, 80°07′W and 29°50.3′N, 80°07′W, respectively).

General discussion

These data represent the most comprehensive assessments of biological, ecological, and distributional information for *C. cornutus* and *C. gymnorhinus*. Data on geographic occurrences, bathymetric distributions, maximum sizes, sizes at maturity, and depth of occurrence are provided for the majority of known specimens of both species that have been collected off the eastern United States. The combined information gleaned from a variety of mostly small collections of these species from this region, including data from specimens reported on in previously published studies and data associated with specimens vouchered in museum collections but for which no previously published information has been available, provides considerable insights into, and comprehensive documentation of, the occurrence, distribution, and natural history of these interesting flatfishes. This updated information, in turn, provides a baseline for evaluating any changes observed in their geographic and bathymetric distributions along the continental shelf off the eastern United States.

In prevailing literature since the late 1960s, the northern extent of the geographic ranges for adult *C. cornutus* and *C. gymnorhinus* has been misreported, resulting in a long history of inaccurate distribution data for these species. Both species are residents on the continental shelf off the southeastern United States off North Carolina and South Carolina, and their persistent presence in this region is documented from nearly a century (*C. gymnorhinus*) to more than a century ago (*C. cornutus*). Occurrences of *C. cornutus* north of North Carolina appear to be irregular, based on the absence of this species in many of the fish community studies conducted in this region (e.g., Grosslein and Azarovitz, 1982; Colvocoresses and Musick, 1984), and based on its generally low frequency of occurrence in the NMFS-NEFSC groundfish surveys conducted annually in this area (J. Galbraith, personal commun.[3]). Gear selectivity in most trawl surveys influences the frequency of occurrence of small-size species in their catches, and many small-size flatfishes, including *C. cornutus* and *C. gymnorhinus*, have often escaped capture or have been misidentified or overlooked in earlier surveys. These factors also likely contributed to the infrequency of reports on these species.

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[3] Galbraith, John. 2009. Woods Hole Laboratory, Northeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 166 Water Street, Woods Hole, MA 02543.

Recent captures of these species—*C. cornutus* from off Hudson Canyon (Fahay, 2007) and the shelf off New York (Steves et al., 1999) and *C. gymnorhinus* from off North Carolina (Quattrini and Ross, 2006; this study) in areas north of their perceived adult geographic ranges—could have been misinterpreted as evidence for expanding geographic distributions (i.e., poleward range extensions) in response to global warming because some marine fishes respond to oceanic warming with shifts in their latitudinal range (for further discussion on this topic in relation to marine fishes see Perry et al., 2005; Nye et al., 2009). However, adult specimens captured nearly a century or more ago, as well as historical literature documenting occurrences of both adults and larvae of these species in these northern locations, prove that these species were present in these areas historically. Similarly, purported new records of reef fishes off North Carolina were probably mistakenly attributed to ocean warming (Parker and Dixon, 1998), when in fact many of those species were already known from the area (see comments in Quattrini and Ross, 2006). These examples clearly indicate a need for more careful research and the need for examination of historical data (published and unpublished) before invoking climate-change hypotheses to explain observed distributional patterns of marine organisms, especially for species that are less well known. Available data indicate only sporadic and infrequent occurrence of adult *C. cornutus* on the continental shelf north of North Carolina, and no records exist of adult *C. gymnorhinus* from north of North Carolina. Changes in the distributions of these diminutive flatfishes on the northwest Atlantic shelf in response to climatic factors may be signaled by northward extension in their geographic ranges, by increases in frequency of capture and prevalence within northern portions of their ranges, or by increases in their biomass in deeper areas within their ranges, as has been observed for other North Atlantic fish species (Dulvy et al., 2008; Nye et al., 2009). The updated baseline information contained herein on the frequencies of occurrences, relative abundances, and detailed examination of bathymetric and geographic ranges of both flatfish species provides the basis for comparison with future evaluations of the responses of these species to changes occurring on the continental shelf of the western North Atlantic Ocean.

Several factors likely contributed to inaccuracies in geographic distributions for these species appearing in recently published literature. Given that these flatfishes are not usually taken in abundance, nor are they commercially important, significant captures could be overlooked in studies of fish communities or commercial fisheries. Important distributional information for both species also have escaped notice because incidental captures of these diminutive flatfishes were often buried in tables or appendices and the significance of these records was not emphasized in the works documenting these captures. Confusion in identifying these species also occurs (e.g., Goode and Bean, 1895; Hildebrand, 1941) and misidentifications in the literature and in museum collections and databases have contributed to oversights of important specimens. Furthermore, studies in which the ecology or distribution of these species was summarized (Gutherz, 1967; Robins and Ray, 1986; Munroe, 2003; McEachran and Fechhelm, 2005; Lyczkowski-Shultz and Bond, 2006; and others) did not contain earlier published records. Unfortunately, the incomplete, and sometimes inaccurate, information contained in these synthetic studies has subsequently been perpetuated in other publications. As biology and ecology disciplines increase the use and reliance on web-based and web-available references, historically important, but less available, less popular, or more obscure literature will be increasingly overlooked. We caution that sole reliance on popular citation sources for historical information, in many cases, is a poor substitute for first-hand examination of all of the pertinent original literature related to a subject. Additionally, regardless of what popularly cited literature sources report, or even what museum databases indicate on their websites, these are no substitutes for actually examining specimens and analyzing collection data associated with them. In our study, nine different references noted the occurrence of *C. cornutus* on the continental shelf south of Rhode Island or off New Jersey and New York, yet all of these publications were disregarded in all but one contemporary literature source for this species.

Moreover, museum specimens represent important archived sources of geographic and bathymetric information. Museum lots of both *C. cornutus* and *C. gymnorhinus* collected over 100 and 92 years ago, respectively, voucher occurrences of adults of these species from the northernmost regions of their geographic ranges. These specimens, too, were overlooked by the same popularly cited studies mentioned above.

Accurate records of geographic occurrence and bathymetric distribution for species such as these two diminutive flatfishes are necessary and important because they provide the background information required to evaluate future changes in their distributions or occurrences in relation to large-scale changes in oceanic conditions on the continental shelf of the western North Atlantic. Changes in distributions of organisms are relevant for assessments of effects of climate change, and more information is needed on the regional dynamics of populations over time to better understand effects of various environmental conditions on their survival and persistence within an area (Nye et al., 2009; Tolan and Fisher, 2009; Wood et al., 2009). Changes in the spatiotemporal occurrences of small-size, noncommercial species often are overlooked or disregarded (Link, 2007). But changes in geographic and bathymetric distributions and relative abundances for such species may provide additional evidence of larger-scale environmental changes impacting biological communities that inhabit the continental shelf off the eastern United States and elsewhere. Without proper understanding of historical data describing distributional patterns, it will be impossible to accurately document any changes that may occur, or be occurring, in the geographic or ecological distributions of such species that inhabit particular geographic regions.

While assembling this information, we updated identifications of museum specimens, located important specimens in a variety of fish collections, and corrected and updated incomplete geographic records for some museum specimens. For both *C. cornutus* and *C. gymnorhinus*, much still remains to be learned about their biology and distributions, especially for a population, or populations, on the continental shelf off the southeastern United States. Age and growth, reproduction, habitat preferences, and trophodynamics remain virtually unknown for these diminutive species. Sadly, this situation is also true for most of the small fishes or those that are not economically important, and as management agencies move toward ecosystem-based, rather than single-species management approaches, data on the whole community becomes even more critical. We urge agencies and academic communities to expand the scope of fishery studies to address this need.

Additional material not included in appendices 1–2

C. gymnorhinus. Larvae: ARC 24522, 32°58′37″N, 77°51′53″W; ARC 24538, 33°24′07″N, 76°42′33″W; MCZ 77935, 41°33′N, 54°55′W.

C. cornutus. Adults. AMNH 86095, *n*=103; AMNH 86160, *n*=43; AMNH 86101, *n*=100; AMNH 84815, *n*=63; AMNH 84857, *n*=47; AMNH 85590, *n*=172; AMNH 85529, *n*=321.

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Appendix 1

List of specimens, collection data, life history information, and associated ecological data for *Citharichthys cornutus* from the continental shelf off the eastern United States and nearby areas of the eastern Caribbean Sea. SL=standard length, *=not examined; **depth estimated from nautical chart; NA=not available N=number of specimens.

Catalogue number	Field number	N	Size range (mm SL)	Males (mature)	Females (mature)	Depth (m)	Latitude (N)	Longitude (W)	Location	Collection date
Uncatalogued	HB 2009-01 Sta. 162	1	72.0	1 (1)	0	132	40°05.593′	70°42.75′	NJ	23 Mar 2009
Uncatalogued	Alb 2006-02 Sta. 107	1	81.3	0	1 (1)	129	40°04.428′	70°40.428′	NJ	25 Feb 2006
Uncatalogued*	FH Sta. 871	1(?)	NA	NA	NA	212	40°02′54″	70°23′40″	NJ	4 Sep 1880
USNM 26003	FH Sta. 870	3	48.4–55.6	3 (3)	0	285	40°02′36″	70°22′58″	NJ	4 Sep 1880
Uncatalogued	HB 2009-05 Sta. 58	2	47.5–49.4	2 (1)	0	113	35°17.872′	70°42.75′		18 Sep 2009
VIMS 2539	Eastward E1-73	2	56.5–64.0	1 (1)	1 (1)	108	34°56.2′	75°23.0′	NC	18 Apr 1971
Uncatalogued	Alb 2007-03 Sta. 48	1	41	1 (1)	0	151–171	34°54′	75°43.4′	NC	12 Mar 2007
Uncatalogued	Alb 2008-01 Sta. 110	3	51.8–53.9	2 (2)	1 (1)	142	34°42.433′	75°35.974′	NC	23 Mar 2008
VIMS 1131	NA	2	51.9–59.6	1 (1)	1 (1)	230	34°36.06′	75°40.6′	NC	18 Apr 1971
Uncatalogued	HB 2009-05 Sta. 54	12	52.5–64.2	9 (8)	3 (3)	107	34°31.096′	75°48.917′	NC	18 Sep 2009
VIMS 11786	Alb 84-02 Sta. 29	1	37	1 (0)	0	158–165	34°19′	75°56′	NC	4 Mar 1984
NCSM 47664	DE-04-008	314	20.0–68.0	177 (164)	137 (121)	123–127	33°25.389′	77°02.234′	SC	18 Apr 2004
AMNH 76925	GMBL 78-135	24	22.0–68.4	NA	NA	117	33°22.5′	77°48.5′	SC	10 Sep 1978
NCSM 47663	SJ 03-007	3	36.5–51.9	3 (3)	0	140	33°20.354′	77°17.025′	SC	18 Aug 2003
USNM 45676	ALB 2417	1	54.7	0	1(1)	174	33°18′30″	77°07′	SC	2 Apr 1885
Uncatalogued*	MARMAP 75206	3	51.6–77.4	NA	NA	159	33°18′	77°08.5′	SC	1975
GMBL 2955	GMBL 73-324	3	64.7–67.0	2 (2)	0	157	33°04.5′	77°40′	SC	15 Nov 1973
Uncatalogued*	MARMAP 73432	4	60.2–68.8	NA	NA	155	33°04′	77°41′	SC	1973
Uncatalogued*	MARMAP 75092	30	17.2–70.2	NA	NA	115	33°03.7′	77°45′	SC	1974
USNM 151887	ALB III 21	1	71.2	1 (1)	0	179	33°03′30″	77°37′	SC	27 May 1949
GMBL 2957	GMBL 73-326	8	31.4–49.0	8 (6)	0	110	33°02.8′	77°53′	SC	16 Nov 1973
Uncatalogued*	MARMAP 75091	7	17.2–60.2	NA	NA	102	33°02.5′	77°53.7′	SC	1974
AMNH 220899*	AT-72-01 Sta. 160	2	NA	NA	NA	147**	32°59′	77°50′	SC	3 Dec 1972
GMBL 02958	GMBL 76-253	2	29.3–43.6	1 (2)	0	137	32°58′	77°52.3′	SC	3 Sep 1976
Uncatalogued*	MARMAP 75198	26	43.0–68.8	NA	NA	139	32°55′	77°57′	SC	1975
MCZ 59549	DE II 81-02 Sta. 56	1	79.1	1 (1)	0	193	32°54′	77° 51′	SC	25 Mar 1981
Uncatalogued*	MARMAP 75195	5	25.8–43.0	NA	NA	81	32°42.5′	78°26.5′	SC	1975
Uncatalogued*	MARMAP 75196	12	60.2–77.4	NA	NA	172	32°40′	78°21.5′	SC	1975
Uncatalogued*	MARMAP 75192	15	25.8–51.6	NA	NA	71	32°30.5′	78°45.3′	SC	1975
GMBL 2956*	GMBL 73-300	1	32	NA	NA	74–77	32°21′	78°58′	SC	9 Nov 1973

continued

Appendix 1 (continued)

Catalogue number	Field number	N	Size range (mm SL)	Males (mature)	Females (mature)	Depth (m)	Latitude (N)	Longitude (W)	Location	Collection date
AMNH 76428*	GMBL 73-298	1	37	NA	NA	86	32°13′	79°06′	SC	9 Nov 1973
USNM 156468	Pelican 182-6	1	60	1 (1)	0	110	32°06′	79°14′	SC	4 Feb 1940
Uncatalogued*	MARMAP 73434	12	25.8–51.6	NA	NA	110	32°02.5′	77°53′	SC	1973
Uncatalogued*	MARMAP 75115	6	60.2–68.8	NA	NA	95	31°44.5′	79°30′	GA	1974
Uncatalogued*	MARMAP 75111	1	43	NA	NA	68	30°54.5′	80°00′	GA	1974
Uncatalogued*	MARMAP 75110	1	60.2	NA	NA	137	30°48′	80°01′	GA	1974
FMNH 74497	SB 3442	2	68.0–70.5	2 (2)	0	155	29°40′	80°12′	central FL	24 Sep 1961
Uncatalogued*	MARMAP 73375	1	68.8	NA	NA	86	29°29.5′	80°15′	FL, Atlantic	1973
AMNH 76357*	GMBL 73-268	3	51.5–52.0	NA	NA	98–110	29°26′	80°12.3′	FL	30 Oct 1973
Uncatalogued*	MARMAP 73376	3	43.0–51.6	NA	NA	110	29°25.6′	80°12′	FL	26 May 1905
FMNH 74493	SB 2476	1	55.0	1 (1)	0	183	25°22′30″	79°14′30″	Northern Bahamas	8 Nov 1960
FMNH 74490	SB 2390	1	63.1	1 (1)	0	91	24°42′30″	80°44′	FL Keys	26 Oct 1960
FMNH 74492	SB 2470	4	51.8–64.6	2 (2)	2 (0)	229	24°25′	79°13′	Straits FL, off Keys	7 Nov 1960
UF 132882*	SB 2445	2	NA	NA	NA	254	24°08′	80°08′	Straits FL, near Bahamas	3 Nov 1960
USNM 282787	SB 2447	7	45.7–61.3	3 (1)	4 (4)	165–229	24°00′	80°25′	Straits FL	3 Nov 1960
USNM 117039	Longley coll.	1	61.5	1(1)	0	250–287	NA	NA	FL, Dry Tortugas	26 Jun 1932
USNM 117094	Longley coll.	16	50.2–65.3	13 (13)	2 (2)	NA	NA	NA	FL, Dry Tortugas	NA
USNM 282789	SB 2464	24	48.7–76.5	15 (6)	9 (8)	274	23°34′	79°05′	Bahamas	6 Nov 1960
Uncatalogued*		1	61.8	NA	NA	250	23°15′04″	81°10′08″	Cuba	19 Jun 1965
USNM 214325	OR II 10861	1	76.5	1 (1)	0	276	23°12′	78°49′	Bahamas	15 Dec 1969
GMBL 3001	GMBL 61-030;SB 3510	3	57.5–73.5	0	2 (2)	276	22°55′	78°36′	Bahamas	1961
USNM 282786; FMNH 74389	OR 2684; OR 2654	7	64.8–72.5	3 (3)	4 (4)	229	18°26′	67°11′	Puerto Rico	6 Oct 1959
USNM 126172	FH 6063	1	45.8	1 (0)	0	140	18°12′22″	67°08′20″	Puerto Rico	20 Jan 1899
USNM 282783	OR 6700	1	70.4	1 (1)	0	249–285	17°27′	62°04′	Caribbean, Antigua	19 May 1967
UF 142601	OR 5067	1	79.3	0	1 (1)	258–267	17°04′	62°39′	Caribbean, St. Kitts	30 Jul 1964
UF 142602	OR 5068	1	78.5	0	1 (1)	258–268	17°04′	62°39′	Caribbean, St. Kitts	31 Jul 1964

Appendix 2

List of specimens, collection data, life history information, and associated ecological data for *Citharichthys gymnorhinus* from the continental shelf off the eastern United States and nearby areas of the eastern Caribbean Sea. SL=standard length; NA=not available; *=not examined. N=number of species.

Catalogue number	Field number	N	Size range (mm SL)	Males (mature)	Females (mature)	Depth (m)	Latitude (N)	Longitude (W)	Location	Collection date
Uncatalogued	HB 2009-05 Sta. 47	1	44.3	1 (1)	0	74	35°05.51′	75°17.24′	NC	17 Sep 2009
Uncatalogued	ALB 1997-06 Sta. 50	6	35.0–46.0	6 (6)	0	59–76	34°39′	75°43′	NC	13 Sep 1997
Uncatalogued	ALB 2008-03 Sta. 109	1	Damaged	NA	NA	130	34°37.26′	75°40′59″	NC	23 Mar 2008
Uncatalogued	HB 2009-01 Sta. 45	8	40.5–48.5	5 (5)	3 (3)	72	34°31.99′	75°51.67′	NC	8 Mar 2009
USNM 111520	FH D8249	1	45.4	1 (1)	0	92	34°12	76°04′56″	NC	13 Sep 1914
NCSM 47657	DEII-04-008	1	49.5	1 (1)	0	123–127	33°25.389′	77°02.234′	SC	18 Apr 2004
NCSM 47661	SJ 2002-056	4	33.9–46.5	4 (3)	0	93–140	33°13.324′	77°16.568′	SC	25 Sep 2001
NCSM 47659	SJ 2001-058	9	36.8–46.9	4 (4)	5 (5)	90–133	33°13.240′	77°17.025′	SC	25 Sep 2001
NCSM 47660	SJ 2001-069	1	45.2	1 (1)	0	101–112	33°12.997′	77°16.649′	SC	26 Sep 2001
NCSM 47658	SJ 2001-068	3	32.4–44.6	3 (3)	0	106–113	33°12.507′	77°17.446′	SC	26 Sep 2001
NCSM 47662	SJ 2001-070	23	26.2–44.3	12 (9)	11 (8)	98–102	33°12.411′	77°18.136′	SC	26 Sep 2001
GMBL 4880	GMBL 78-136	16	20.4–44.2	10 (9)	6 (5)	77	33°05.8′	77°48.2′	SC	10 Sep 1978
GMBL 2960	GMBL 73-326	3	24.0–37.6	3 (2)	0	110	33°02.5	77°53′	SC	16 Nov 1973
AMNH 76430; Uncat. 73406*	GMBL 73-298	2	37.2–38.0	NA	NA	86	32°13′	79°06′	SC	9 Nov 1973
USNM 315696	SCMRRI 63800766	1	44.5	1 (1)	0	66	31°31′48″	79°44′24″	GA	12 Sep 1980
Uncatalogued*	NA	5	6.4–24.0	NA	NA	35–48	31°16′	80°01′	GA	28 Jun 2005
Uncatalogued*	MARMAP 74074	1	NA	NA	NA	71	29°09′	80°08.6′	FL	1974
Uncatalogued*	MARMAP 75252	15	NA	NA	NA	70	28°50.3′	80°07′	FL	1975
USNM 203602	SB 3469	1	39.3	0	1 (1)	201	27°23′	78°35′	Bahamas	25 Oct 1961
UF 215588	Gerda 282	1	35.2	0	1 (1)	70–88	25°43′	80°05′	FL Straits	1 Apr 1964
UF 220768	Gerda 752	2	39.2–42.2	0	2 (2)	87–96	25°14′	80°09′	FL Straits	14 Sep 1965
USNM 45610; USNM 45677; USNM 143120	ALB 2318	36	30.1–44.5	28 (26)	8 (7)	83	24°25′45″	81°46′	FL Straits, S. Key West	15 Jan 1885
USNM 129946	ALB 2316	2	41.9–44.7	2 (2)	0	92	24°25′30″	81°47′45″	FL Straits	15 Jan 1885
UF 111098	FFS 99-20	2	39.8–41.0	2 (2)	0	55	24°25′23.5″	82°52′53″	FL Straits	8 May 1999
UF 98623	GHB 92-20	7	43.4–47.1	7 (7)	0	67–71	24°25′05″	82°16′21″	FL Straits	26 Sep 1992
UF 230503; UF 217400	Gerda 566	19	29.0–52.4	9 (9)	10 (10)	64	24°25′	82°55′	FL Straits	12 Apr 1965
UF 36455	JTW 680-10	4	24.2–45.1	3 (2)	1 (1)	64	24°24.34′	81°58.26′	FL Straits	4 Jun 1980
USNM 158279	OR 1004	2	46.5–48.7	2 (2)	0	68	24°24′	82°55′	FL Straits	13 Apr 1954

continued

Appendix 2 (continued)

Catalogue number	Field number	N	Size range (mm SL)	Males (mature)	Females (mature)	Depth (m)	Latitude (N)	Longitude (W)	Location	Collection date
UF 32429	GHB 81-7	1	33.9	1 (1)	0	101–107	24°23′22″	81°55.54′	FL Straits	31 May 1981
UF 116711	GHB 00-04	1	51.6	1 (1)	0	61–62	24°22′47″	82°45′30.3″	FL Straits	10 May 2000
UF 109237	GHB 98-13	1	48.0	0	1 (1)	79–88	24°21′50″	82°36′55″	FL Straits	7 May 1998
UF 217664	Gerda 575	1	39.2	1 (1)	0	64	24°21′	82°34′	FL Straits	13 Apr 1965
UF 219281; UF 217403	Gerda 574	7	20.3–43.7	3 (2)	4 (3)	59	24°21′	82°35′	FL Straits	13 Apr 1965
ex. USNM 117039	Longley Coll.	1	44.5	1 (1)	0	NA	NA	NA	S. Tortugas, FL	26 Jun 1932
UF 19295	SB 2455	2	44.4–45.0	2 (2)	0	166–193	23°34′30″	79°03′	Bahamas	5 Nov 1960
USNM 203603	SB 5165	1	32.7	0	1 (1)	91	19°48′	70°35′	Dominican Republic	15 Oct 1963
FMNH 74443	OR 2616	8	31.7–38.6	7 (7)	1 (1)	75	18°50′30″	64°38′	N. Br. Virgin Islands	27 Sep 1959
FMNH 74442	OR 2615	5	35.7–39.7	4 (4)	1 (1)	73	18°50′30″	64°37′	N. Br. Virgin Islands	27 Sep 1959
FSBC 1559*	OR 2622	2	36.7–39.8	1 (2)	1 (2)	44	18°45′	64°40′	N. of Virgin Islands	28 Sep 1959
FMNH 74387	OR 2624	3	36.4–42.9	2 (1)	1 (1)	69	18°45′	64°47′	N. Br. Virgin Islands	28 Sep 1959
UF 207071	OR 2668	1	43.9	1 (1)	0	70	18°31′	66°47′	Puerto Rico	8 Oct 1959
FMNH 74386	OR 2632	3	48.5–52.1	3 (3)	0	91	17°34′	63°30′	S. Br. Virgin Islands	30 Sep 1959

Age validation of great hammerhead shark (*Sphyrna mokarran*), determined by bomb radiocarbon analysis

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Abstract—Preliminary validation of annual growth band deposition in vertebrae of great hammerhead shark (*Sphyrna mokarran*) was conducted by using bomb radiocarbon analysis. Adult specimens (n=2) were collected and thin sections of vertebral centra were removed for visual aging and use in radiocarbon assays. Vertebral band counts were used to estimate age, and year of formation was assigned to each growth band by subtracting estimated age from the year of capture. A total of 10 samples were extracted from growth bands and analyzed for $\Delta^{14}C$. Calculated $\Delta^{14}C$ values from dated bands were compared to known-age reference chronologies, and the resulting patterns indicated annual periodicity of growth bands up to a minimum age of 42 years. Trends in $\Delta^{14}C$ across time in individual specimens indicated that vertebral radiocarbon is conserved through time but that habitat and diet may influence $\Delta^{14}C$ levels in elasmobranchs. Although the age validation reported here must be considered preliminary because of the small sample size and narrow age range of individuals sampled, it represents the first confirmation of age in *S. mokarran*, further illustrating the usefulness of bomb radiocarbon analysis as a tool for life history studies in elasmobranchs.

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Validation of the periodicity of vertebral growth band deposition over the entire life span of a species is an important aspect of age estimation and growth determination in elasmobranch fishes (Caillet and Goldman, 2004; Francis et al., 2007). Accurate age estimation is critical because it forms the basis for calculating growth and mortality rates, age at maturity, and estimates of longevity, all of which are essential for population assessment. The need for accurate age and growth estimates is especially great for many elasmobranch species, which tend to be data poor and highly vulnerable to fishing pressure (Musick, 1999). Bomb radiocarbon dating has been successfully used to validate age estimates for several elasmobranch species (e.g., Campana et al., 2002; Kneebone et al., 2008; McPhie and Campana, 2009). The peak in atmospheric radiocarbon (^{14}C) from testing nuclear bombs in the 1950s and 1960s is used as a marker that can be dated in the calcified structures of marine organisms. Bomb testing yielded synchronous known-age reference chronologies in corals, bivalves, and fish otoliths worldwide (Campana, 1997; Druffel, 1989), which can be used to confirm the accuracy of age estimates for various marine species (Campana et al., 2002). The presence of a tracer over such a protracted time span makes bomb radiocarbon analysis highly suitable for age validation, especially for typically long-lived elasmobranchs.

The great hammerhead shark (*Sphyrna mokarran*) is a large (maximum size of 550–610 cm total length [TL]) cosmopolitan species found circumtropically in both inshore and oceanic habitats to depths of over 80 meters (Compagno, 1984). Great hammerhead sharks tend to be reef-associated, but some populations undertake seasonal offshore migrations (Compagno, 1984). Life history information for the great hammerhead shark is very limited; reports consist mostly of notes on their reproduction (Stevens and Lyle, 1989). There are no published age validations for *S. mokarran*.

The vulnerability of great hammerhead sharks to fishing pressure is potentially high given the tendency of elasmobranchs to exhibit slow growth, late age at maturity, and low fecundity (Musick, 1999). Although not generally targeted in fisheries, *S. mokarran* are favored among incidentally caught species because their fins are highly valued due to their size and the density of their fin rays. In an assessment of the Hong Kong shark fin market, it was found that fins from hammerhead shark species were among the most valuable fin types in the market (Clarke et al., 2004; Abercrombie et al., 2005). Recently, concern has arisen in regard to populations of *S. mokarran* worldwide because the International Union for Conservation of Nature (IUCN) assessed the species as endangered.[1] These circumstances illustrate the need for validated age estimates of *S. mokarran*. Here, we present the preliminary results of bomb radiocarbon analysis as a novel and accurate method of age validation for this species.

Materials and methods

Vertebrae for bomb radiocarbon age validation were taken from two *S. mokarran* specimens (SM-112 and SM-114) caught from commercial longline vessels off the Georgia coast in the U.S. south Atlantic between 2003 and 2004. Specimens were both male, measuring 300 cm and 276 cm fork length (FL), respectively. Although *S. mokarran* are frequently caught as bycatch in several commercial and recreational fisheries, it is difficult to obtain vertebral samples from individuals of sufficient age for the purposes of this study. Ideally, specimens would have vertebral tissue formed between 1955 and 1965, the years encompassing the period of initial increase in ^{14}C (Campana et al., 2002; Piner et al., 2005). However, individuals living during this time period would at present be quite large (>300 cm FL) and the occurrence of specimens of this size are infrequent in catches available for sampling. The two specimens used in this study provided the only vertebral samples of appropriate age available to the authors at the time of this study.

Vertebrae were collected either from the area under the dorsal fin or above the branchial chamber, stored on ice, and later frozen upon arrival at the laboratory. Excess tissue was manually removed from thawed vertebrae, which were then soaked in varying concentrations of sodium hypochlorite solution for 5–30 minutes to remove remaining tissue. Cleaned vertebrae were rinsed in tap water and stored in 70% ethanol. Vertebral sections (1 mm thick) were prepared by a single longitudinal cut with paired blades separated by a spacer on an IsoMet low-speed diamond-bladed saw (Buehler, Lake Bluff, IL). Sections were immersed in ethanol and digitally photographed under a binocular microscope at 16–40× magnification with reflected light. Age interpretation was based on visual counts of paired growth increments (growth bands) from images enhanced for contrast with Adobe Photoshop CS2 (Adobe Systems, Inc., Burlington, NJ), and interpretation was based on the criteria of Natanson et al. (2002).

Vertebral tissue samples (n=10 samples; 4–9 mg each) were extracted from multiple growth bands in the corpus calcareum region of each vertebral section. Extractions were performed under the binocular microscope with 16× magnification. Extracted samples were isolated as solid pieces by using a Gesswein high-speed hand tool (Gesswein, Bridgeport, CT) fitted with steel bits <1 mm in diameter. The first-formed growth band (corresponding to the first year of growth) was extracted from each vertebra; individual growth bands corresponding to later years were also extracted. The samples from both specimens corresponding to the most recent growth (where growth bands were very narrow) consisted of 6–10 pooled growth bands. The presumed date of sample formation (i.e. growth band formation) was calculated as the year the shark was collected minus the growth band count from the birth band to the mid-point of the sample. After sonification in Super Q water and drying, the sample was weighed to the nearest 0.1 mg in preparation for ^{14}C assay with accelerator mass spectrometry (AMS). AMS assays also provided Δ^{13}C (‰) values, which were used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as Δ^{14}C, which is the per mil (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay before 1950 according to methods outlined by Stuiver and Polach (1977).

To assign dates of formation to an unknown tissue sample, it is necessary that the Δ^{14}C of the unknown sample be compared with a Δ^{14}C chronology based on known-age material (a reference chronology). To match the water mass characteristics of *S. mokarran* habitat, we used a reference chronology for Florida corals developed by Druffel (1989). This chronology would be expected to show Δ^{14}C values comparable to those of the great hammerhead shark because of similarity of habitat. However, the carbon source for vertebrae is metabolic in origin unlike the dissolved inorganic carbon (DIC) source for coral (Campana et al., 2002). Therefore, we also used a reference chronology developed from known-age porbeagle (*Lamna nasus*) in the northwest Atlantic (Campana et al., 2002). The period of increase in ^{14}C in this chronology would be expected to be very similar to that of great hammerhead sharks inhabiting the U.S. south Atlantic, although with very different absolute values owing to the different water mixing characteristics of the two regions.

Results

Based on annual growth band counts, the age estimate for each vertebra was 42 years for SM-112 and 36 years for SM-114, yielding birth years of 1961

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[1] Camhi, M. D., S. V. Valenti, S. V. Fordham, S. L. Fowler, and C. Gibson. 2009. The conservation status of pelagic sharks and rays: report of the IUCN shark specialist group pelagic shark Red List workshop, 78 p. IUCN Species Survival Commission Shark Specialist Group, Newbury, UK.

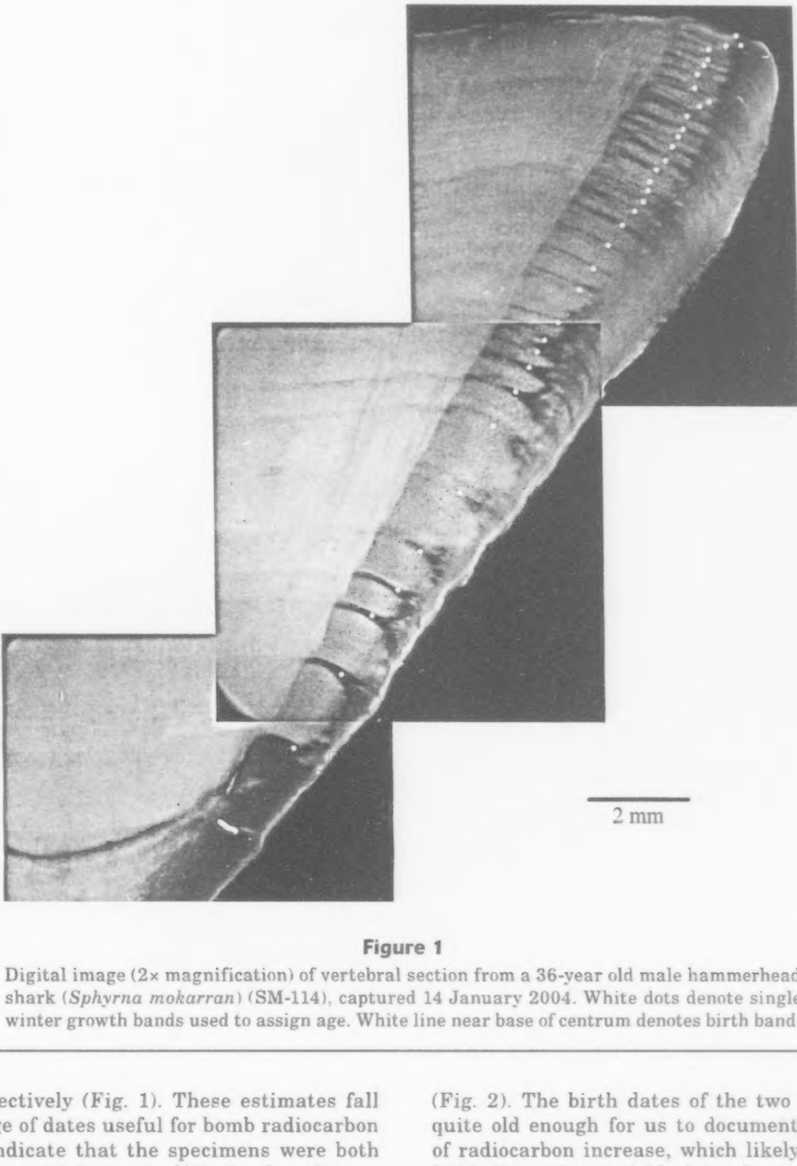

Figure 1

Digital image (2× magnification) of vertebral section from a 36-year old male hammerhead shark (*Sphyrna mokarran*) (SM-114), captured 14 January 2004. White dots denote single winter growth bands used to assign age. White line near base of centrum denotes birth band.

and 1967, respectively (Fig. 1). These estimates fall within the range of dates useful for bomb radiocarbon analysis and indicate that the specimens were both born during the initial rise in ^{14}C. Bomb radiocarbon analysis yielded results for seven samples from SM-112 and three from SM-114 (Table 1). Values of δ^{13}C were relatively stable over the range of samples (mean=−11.0, standard deviation [SD]=0.1) and were similar to those from other elasmobranch species, verifying a dietary (metabolic) carbon source (Fry, 1988; Campana, 1997; Campana et al., 2006). The mean standard deviation of the individual radiocarbon assays was about 5‰.

Values of Δ^{14}C in *S. mokarran* ranged from 18.6 to 148.3 units, reaching a maximum in the early 1970s (Fig. 2). The birth dates of the two sharks were not quite old enough for us to document the initial year of radiocarbon increase, which likely occurred before 1961. Given the available data, the trend in timing and magnitude of the Δ^{14}C chronology for all of the *S. mokarran* samples most closely resembled that of Florida coral. Timing of the period of increase and peak in Δ^{14}C was also similar between *S. mokarran* and porbeagle chronologies, but there were large differences in absolute values.

When trends in Δ^{14}C for the two specimens were examined individually, a difference in trajectories was apparent between SM-112 and SM-114. Values from both specimens fell mostly along the curve of the coral chronology, with one exception. The sample

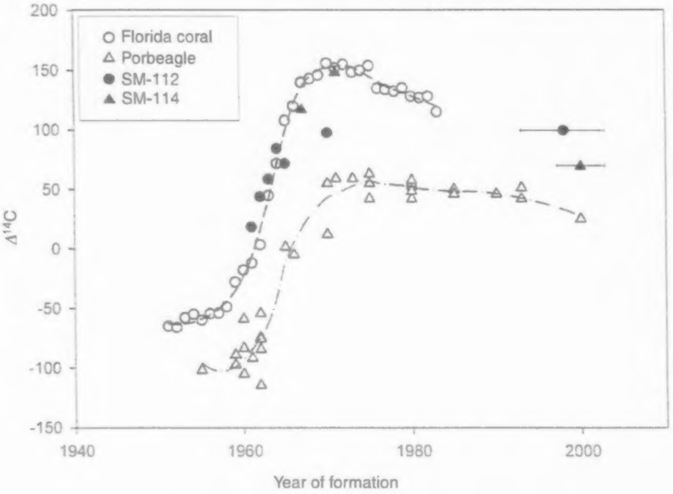

Figure 2

Bomb radiocarbon ($\Delta^{14}C$) values over time in two great hammerhead shark (*Sphyrna mokarran*) individuals (SM-112 and SM-114), compared with Florida coral and porbeagle (*Lamna nasus*) reference chronologies. LOESS (locally weighted regression) curves have been fitted to the Florida coral and porbeagle data series. Terminal points for SM-112 and SM-114 are bracketed to show years of formation for pooled growth bands included in each sample.

Table 1

Summary of age data and bomb radiocarbon analysis for vertebral samples taken from great hammerhead sharks (*Sphyrna mokarran*). Sample SM-112 was male, fork length=300 cm, aged at 42 years, and captured on 23 July 2003. Sample SM-114 was male, fork length=276 cm, aged at 36 years, and captured on 14 January 2004. Year of formation=year of growth-band formation.

Sample	Year of formation	Median year of formation	Estimated age	$\delta^{13}C$	$\Delta^{14}C$
SM-112	1961	1961	0	–11.4	18.6
	1962	1962	1	–11.4	43.9
	1963	1963	2	–11.0	58.7
	1964	1964	3	–10.5	84.4
	1965	1965	4	–9.9	71.9
	1970	1970	9	–9.2	97.7
	1993–2003	1998	37	–10.7	99.7
SM-114	1967	1967	0	–12.0	117.2
	1971	1971	4	–12.0	148.3
	1997–2003	2000	32	–12.2	69.8

dated 1970 from SM-112 fell well below the curve of the coral chronology, whereas the most recent (pooled) sample from SM-112 fell more closely to the expected downward trajectory for Florida coral. Samples from SM-114 were nearly synchronous with the coral chronology extrapolated to the year 2000. Within-shark patterns in $\Delta^{14}C$ accumulation were similar to those of the reference chronologies, confirming that carbon recorded in the vertebrae is conserved through time.

Discussion

Although a larger sample size would have been preferable in this study, the results of the bomb radiocarbon assays support the hypothesis of annual growth band deposition in *S. mokarran* vertebrae. Additionally, the similarity in the timing of increase and peak in $\Delta^{14}C$ between the great hammerhead shark samples and both reference chronologies indicates that the aging techniques employed in this study produce ages accurate to within a few years. It is generally accepted that the timing of the initial increase in $\Delta^{14}C$ in relation to prebomb values is the most accurate dated marker for age validation (Campana et al., 2008). Although there were no prebomb samples in our study (all $\Delta^{14}C$ values were above zero), the close alignment of values between *S. mokarran* samples and those from the coral chronology during the period of increase indicates that our ages were assigned correctly. If the specimens analyzed in this study had been under-aged, the entire great hammerhead shark chronology would have been shifted to the right in relation to the coral chronology, and over-aging would have caused the reverse to be true. No such shifting was apparent.

Differences in both the magnitude and timing of radiocarbon chronologies between vertebral samples and those from carbonate sources have been noted in previous age studies of elasmobranchs. The difference in the magnitude of $\Delta^{14}C$ values is largely attributable to the different carbon sources in carbonate (DIC uptake) compared to cartilaginous (dietary uptake) systems (Fry, 1988), but also to environmental factors such as habitat depth and the mixing rates of waters (Williams et al., 1987). This difference has been demonstrated in porbeagle (Campana et al., 2002), shortfin mako (*Isurus oxyrinchus*) (Ardizzone et al., 2006), and white sharks (*Carcharadon carcharias*) (Kerr et al., 2006), as well as in two species of skates (McPhie and Campana, 2009), and can also be caused by the age of the carbon in prey items found at different depths, which can produce a delay in the radiocarbon chronology. In the case of *S. mokarran*, however, overall values of $\Delta^{14}C$ followed those of Florida coral very closely, indicating little difference in timing of uptake between coral and vertebrae. The similarity in values of $\Delta^{14}C$ is likely due to similarity in habitat for both the coral and the shark; *S. mokarran* are reef-associated for much of their lives (Compagno, 1984) and feed on reef-associated prey (Stevens and Lyle, 1989), which may assimilate carbon more quickly because of the well-mixed shallow habitat. Kneebone et al. (2008) found that young tiger sharks (*Galeocerdo cuvieri*) exhibit similar patterns in $\Delta^{14}C$ uptake, attributing the pattern to a diet of small teleosts during the time that these sharks inhabit shallow nursery grounds. Campana et al. (2006) also found similar results in spines of spiny dogfish (*Squalus acanthias*), in which carbon uptake into fin spines mirrored that of DIC uptake in otolith chronologies from the same region.

Despite the apparent similarities between values of $\Delta^{14}C$ in *S. mokarran* and Florida coral, there were some differences, such as the slight left shift in the first two samples from SM-112 and the depletion of $\Delta^{14}C$ in the penultimate (1970) sample from SM-112, in relation to the rest of the chronology. The first two samples from SM-112, corresponding to formative years of 1961 and 1962, respectively, fell slightly left of the coral curve. Although a phase-shift to the right can be explained as a diet- or habitat-induced delay in carbon uptake, a shift to the left could indicate a slight over-aging of SM-112 of only 1–2 years, or the shift could be the result of inclusion of material from more recently formed bands in the sample. In addition, the $\Delta^{14}C$ in the 1970 sample from SM-112 was depleted in comparison to the rest of the chronology and approached values more like those of porbeagle as opposed to coral. This singular deviation could again be the result of an error in micromilling or could be the start of a more depleted trajectory for SM-112, reflecting an ontogenetic shift in habitat and diet. Although reef-associated for much of their lives, *S. mokarran* also undertake oceanic migrations through deeper water habitats (Compagno, 1984) that tend to be depleted in $\Delta^{14}C$. Consumption of prey from these habitats would result in depleted values of $\Delta^{14}C$ in the vertebrae, as demonstrated in porbeagle and other deepwater sharks (Campana et al., 2002). Another possibility for this depletion in $\Delta^{14}C$ is a shift in age of prey taken by SM-112; owing to its size this shark may have taken larger (and possibly older) prey. Obtaining additional $\Delta^{14}C$ samples from both sharks would certainly clarify these results.

This study confirms the longevity of great hammerhead sharks to an age of at least 42 years, although maximum reported lengths indicate that they may live well beyond this age. Further study on the life history of *S. mokarran* is needed to identify factors affecting individual patterns in $\Delta^{14}C$ assimilation.

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Use of stereo camera systems for assessment of rockfish abundance in untrawlable areas and for recording pollock behavior during midwater trawls

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Abstract—We describe the application of two types of stereo camera systems in fisheries research, including the design, calibration, analysis techniques, and precision of the data obtained with these systems. The first is a stereo video system deployed by using a quick-responding winch with a live feed to provide species- and size-composition data adequate to produce acoustically based biomass estimates of rockfish. This system was tested on the eastern Bering Sea slope where rockfish were measured. Rockfish sizes were similar to those sampled with a bottom trawl and the relative error in multiple measurements of the same rockfish in multiple still-frame images was small. Measurement errors of up to 5.5% were found on a calibration target of known size. The second system consisted of a pair of still-image digital cameras mounted inside a midwater trawl. Processing of the stereo images allowed fish length, fish orientation in relation to the camera platform, and relative distance of the fish to the trawl netting to be determined. The video system was useful for surveying fish in Alaska, but it could also be used broadly in other situations where it is difficult to obtain species-composition or size-composition information. Likewise, the still-image system could be used for fisheries research to obtain data on size, position, and orientation of fish.

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For modern fisheries stock assessments, fisheries-independent data are necessary to estimate population abundances and population trends. For most marine species, fisheries-independent abundance estimates are primarily obtained from large-scale multispecies bottom trawl surveys (e.g., Gunderson and Sample, 1980) and from acoustic surveys of pelagic fish stocks (e.g., Karp and Walters, 1994). Although acoustic backscatter is used to measure fish abundance, midwater trawl samples are needed to determine the size and species composition of acoustically sampled fish populations. Both of these survey methods require physical sampling of trawl catches and such sampling can result in unrepresentative data in several ways.

Bottom-trawl surveys are limited to the areas they can sample because many research trawls are not constructed to efficiently fish over a rough or rugose seafloor. Thus, surveys with bottom trawls may not be appropriate for some species with affinities for untrawlable habitat or in survey areas where significant patches of untrawlable ground can be found (Zimmermann, 2003; Cordue, 2007). In Alaska, semipelagic species such as northern rockfish (*Sebastes polyspinis*) and Pacific ocean perch (*S. alutus*) are an important part of the commercial catch, but they also show some affinity for untrawlable areas (Clausen and Heifetz, 2002; Rooper et al., 2007).

In addition, inferences from species- and size-composition data obtained from trawl catches can be biased on account of trawl selectivity. Trawls are generally designed to capture larger, market-size fish, and their design for this selected size results in the under-retention of juvenile size classes. In acoustic surveys of walleye pollock (*Theragra chalcogramma*), biases in midwater trawl catches directly translate into biases in abundance estimates for areas where large and small fish are found (Godo et al., 1998). Selective retention of fish is a consequence of size and species-dependent fish behavior during the trawling process. Observation of fish reactions to trawl gear is critical to understanding the behavioral mechanisms responsible for trawl selectivity and to develop future trawl gear for research.

Here, we describe the use of stereo photography to sample rockfish in untrawlable habitats using a drop unit with a stereo video camera (hereafter termed "video-drop" camera), and to study fish behavior in midwater trawls using a trawl-mounted pair of still-frame stereo cameras (hereafter, termed "still-frame" camera). Stereo cameras have been successfully used to measure fish in controlled aquaculture settings (Ruff et al., 1995; Harvey et al., 2003) and in open water

Table 1

Design, manufacturer, and cost (approximate estimates in U.S. dollars) for drop stereo-video camera and still-frame stereo-camera systems used for surveying untrawlable habitat and studying fish behavior in midwater research trawls. Both systems were used in the field in July 2008 and July 2007, respectively. HID=high-intensity discharge; LED=light-emitting diode; UHMW = ultra high molecular weight plastic.

System	Component	Design	Manufacturer	Cost
Drop stereo-video camera	HID light	HID Xenon lights, 12 V, 50 W	Underwater Lights USA	$814
	Video line driver	Balanced line driver and transceiver	Nitek	$133
	Conducting cable	4 conductor wire, 4.72 mm diameter	Rochester Cable	$1601
	Sled frame	Aluminum channel and tubing	Local manufacture	$2000
	Winch and slip ring	CSW-6 electronic win	A.G.O. Environmental	$11,268
	Underwater housings cameras	5″ diameter	Local manufacture	$729
	Underwater housings lights	—	Local manufacture	$729
	LED sync	—	Ramsey Electronics	$24
	Underwater cable and connections	—	Teledyne Impulse	$614
	Batteries	4×12 V 4 Ah NiMH	Energy sales	$396
			Total video system cost	$18,308
Still-frame stereo camera	Strobe	Oceanic 3000	Oceanic	$990
	Cameras	Canon Digital Rebel Xt (8Mp)	Canon USA	$1100
	Lenses	Canon EF 28 mm f/2.8	Canon USA	$450
	Microcontroller & circuitry	—	Local manufacture	$150
	Underwater housings and viewports	10″ floats, 1.5″ acrylic flat viewports	Local manufacture	$1400
	Mounting frame	UHMW plastic and aluminium stock	Local manufacture	$350
	Underwater connections	—	Teledyne Impulse	$650
	Batteries	3×12 V 4 Ah NiMH	Energy sales	$297
			Total still-frame system cost	$5387
	Software	Matlab V 7.6	Mathworks	

(i.e., van Rooij and Videler, 1996; Shortis et al., 2009). The recent development of high-resolution digital cameras has vastly improved the performance and reduced the complexity of image-based sampling because high-quality digital images can be directly analyzed with image-processing software. In general, stereo methods provide highly precise measurements in comparison to single-camera–based photogrammetric methods (Harvey et al., 2002). However, these systems necessitate maintaining a stable two-camera geometry and must be initially calibrated with targets of known sizes. Despite these constraints, stereo photography is widely used in optical-based sampling in a variety of marine studies.

We demonstrate the precision of stereo-camera–based measurements, attainable from initial deployments in the field, in comparison with traditional survey measurements. The results show that stereo-based optical sampling is a viable method for augmenting bottom-trawl data for abundance estimations; the stereo cameras allow scientists to survey sampling areas that are unavailable to standard survey trawl gear. In addition, stereo cameras can be used to observe and quantify the behavior of fish in the process of being captured by trawl gear to further improve estimates of abundance because they allow scientists to determine the potential biases in trawl-based catch data.

Materials and methods

Sampling untrawlable areas with the video-drop camera system

The design of the video-drop system was based on two key needs. Because rockfish are found in areas of high relief, the camera needed to have adequate protection for their electronic components and have the ability to maintain visual contact with the bottom through rough substrate areas. Therefore, essential to sampling with this camera system was the ability to live-view the video and the use of a quick-responding winch system that could be controlled by the operator aboard the research vessel. The specifications of the camera components are presented in Table 1.

The winch used to deploy and retrieve the camera system and navigate the seafloor was a CSW-6 multipurpose win (A.G.O. Environmental, Nanaimo, BC, Canada; Fig. 1A). The winch motor was a $^3/_4$ horse-

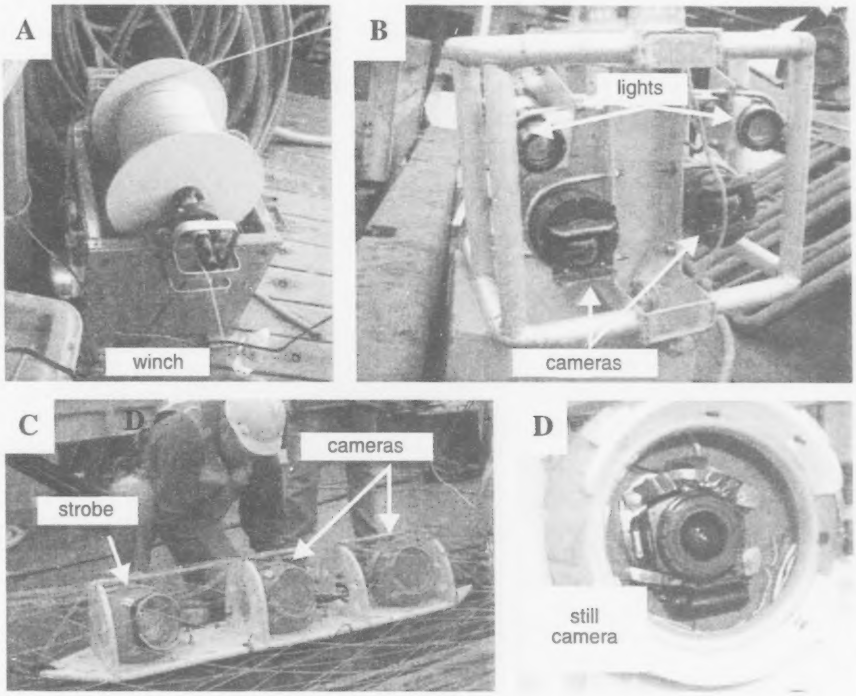


Figure 1

Drop stereo-video camera system showing (**A**) the quick-responding winch, and (**B**) the locations of cameras and lights in the aluminum frame. (**C**) The still-frame camera system, which is deployed in a midwater trawl. (**D**) The camera housings (shown) were constructed from deep-water trawl floats which provided buoyancy and reduced the weight of the cameras.

power Leeson wet-duty motor powered by 100 V AC. The winch speed ranged from 43 m/min (with a bare drum) to approximately 58 m/min (with a full drum). The approximate square-in area of the winch was 48 in^2 (0.031 m^2) and its weight was 155 lb (70.3 kg). The drum was 16 in (40.6 cm) in circumference and was filled with 1312 ft (400 m) of 3/16-in (4.72-mm) conducting wire. The wire had a breaking strength of 3300 lb (1497 kg) and was connected to the camera sled with a cable-grip. The video feed from the cameras was passed up a cable and through a four-conductor slip ring mounted on the winch and routed into a junction box where it was connected to a monitor for real-time viewing.

The protective cage around the camera and lights was constructed of 1.5-in (3.81-cm) aluminum tubing, and the interior members of the frame were composed of 6-in (15.24-cm) aluminum channel (Fig. 1B). A tail chain was attached to the rear of the ventral surface of the cage to drag along the seafloor to help keep the camera unit in contact with the seafloor and oriented forward during deployment. The tail chain was connected to the cage by a short piece of twine to act as a "weak link" in case the tail chain snagged on the seafloor.

The underwater video was recorded by two identical Sony TR-900 camcorders (Sony Electronics Inc., San Diego, CA) located inside the camera housings. The cameras were capable of collecting 720 p progressive scan video images at a resolution of 720×480 pixels. The video was recorded to digital video tapes for a maximum of one hour per tape. Because the cable was too long (400 m) to transmit a standard video signal, it was transformed by using a video balun (in the camera housing) and a receiver (at the winch) to reconvert the video signal back to a viewable picture of the seafloor to use for real-time navigation. Cameras were placed in separate housings constructed of titanium tubing and that had a glass dome port (pressure-rated to 3000 m depth) covering the lens. The lens of each camera was keyed to its port to prevent the camera from being inserted into the housing in a position other than the exact keyed position and stabilized the relative position of the cameras from deployment to deployment—an important consideration for accurate measurement of targets (Shortis et al., 2000). The housings were mounted side by side on the aluminum frame (Fig. 1B).

Illumination was provided by two lights mounted above the camera housings inside the aluminum frame (Fig. 1B). The lights were 50-watt high-intensity discharge (HID) Xenon lights with 5300 lumen output and 3900 Kelvin color temperature. The lights were inserted into 3-in (7.62-cm) diameter titanium housings and the entire light weighed 5 lb (2.27 kg). The lights were powered by a battery located in the camera housing and linked to the light housing by underwater connectors. Four rechargeable 4 Ah 12 V nickel-metal hydride batteries were connected in parallel to provide approximately 1.5 hour of light per deployment. Each light housing was mounted on an adjustable mount that allowed even illumination of the target.

Observing fish behavior in a trawl with the still-frame system

The still-frame system was designed to be light and small enough to be easily attached to the inside of a survey trawl without significantly changing the fishing activity of the net. The system also needed to provide adequate illumination and resolution in order to allow the fish inside the net to be observed at a range of up to 6 m as they passed though a midwater survey trawl 40 m ahead of the codend. A pair of Canon Rebel Xt 8 megapixel digital single-lens reflex cameras (Canon USA, Lake Success, NY) were used to capture fish images. Both cameras were outfitted with 4-gigabyte compact flash memory cards for storage of the images. A high-power wide-angle Xenon strobe (90°, 150 W/s) was used to illuminate the field of view. Three 4-Ah 12 V batteries were mounted in the strobe housing; two were connected to the strobes and the third was used to power the cameras.

The cameras were mounted in separate housings made from 10-in (25-cm) diameter deep-water–rated (1800 m) trawl floats. Images were taken though a 25-mm thick flat acrylic viewport. The strobe and batteries were mounted in a third float housing (Fig. 1C). All three float housings were secured on a sled constructed of 25-mm thick plastic plate and aluminum rails for protection. The approximate weight of the complete assembly in air was 30 kg and was positively buoyant because of the float housings. Quick-release trigger snaps were attached to the ends of the plastic mounting board for attachment to the inside of the trawl. The cameras were aimed across the trawl, perpendicular to the water flow to provide lateral views of fish passing by. The trigger on the camera shutter was controlled by using a microprocessor that was programmed for the study and that located in one of the camera housings. A two-axis tilt sensor was attached to the microprocessor board to allow measurements of fish tilt (deviation of snout-tail axis from the horizontal) and yaw (angle of fish heading in the horizontal plane) to be adjusted from being relative to the camera platform to being in absolute orientation. A pressure switch was used to activate the system once the depth exceeded 20 meters. Images were taken at intervals of 5 s to reduce the influence of light on fish behavior and to ensure that a new group of fish was observed in each frame. The system was capable of taking about 400 images or operating for 33 min of trawl time per deployment.

Calibration of the two types of stereo cameras

The same calibration procedure was used for both stereo-camera systems. The basic procedure required collecting images of a target plate with a printed 10×10 square checkerboard pattern of known dimensions (50×50 cm squares for the video-drop system, 100×100 cm for the still-frame system). This calibration was performed underwater. The video-drop system cage was suspended in the water while the research vessel was secured to the dock. The approximate depth of the camera was 1 m and the distance from the target was 2 m. The checkerboard target was lowered into the water along the vessel until it was plainly visible in both cameras. The target was then slowly moved horizontally and vertically through the field of view of both cameras. Up to 15 min of calibration video was collected by this method. For the still-frame system, an external trigger cable was attached to the assembly, and the system slowly moved about while capturing images of the fixed checkerboard plate.

To calibrate the video-drop system, progressive scan video images were collected at 29.97 frames/s in each camera, and the beginning of the video feed from each camera was aligned by using a light-emitting diode (LED) synchronization light at the beginning of deployment. This process was repeated at the end of the deployment to confirm that the video frames were still aligned. For the calibration procedure, still frame images were extracted from the aligned video at 1-s intervals with Adobe Premier software (Adobe Systems, Inc., San Jose, CA). Synchronization was not necessary for the still-frame system because the cameras were triggered simultaneously. Approximately 20 paired images where the target checkerboard was visible in both cameras were randomly selected for the calibration of each camera system.

The calibration parameters were estimated with the camera calibration toolbox in Matlab, a freely available software analysis toolbox built with Matlab computing language (Mathworks, Inc.; Bouget, 2008; Fig. 2). For each image pair, the position of the corner points of the checkerboard pattern were identified by clicking on the images and the location of these points in the still images was computed by the calibration software to determine the intrinsic parameters of each camera. Intrinsic parameters were used to correct the individual images for optical distortion resulting from the camera lenses. The checkerboard pattern allowed the software to automatically pinpoint exact corner locations based on the color contrast of the square boundaries, making the initial precision of the manual clicking less critical.

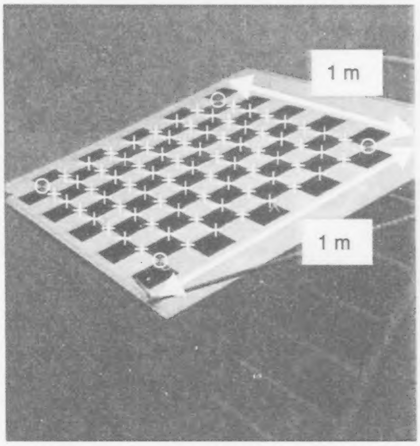


Figure 2

The checkerboard pattern used to calibrate and test the drop stereo-video camera and the still-frame stereo-camera systems. Images used for calibration were processed by using the camera calibration toolbox written for Matlab. An image taken by the still-frame stereo-camera system is shown with the user-selected extreme corners shown as white circles and the automated extraction of all intermediate corners shown with white crosses. This procedure was repeated for up to 20 different images with both systems.

Stereo calibration required that the checkerboard corners be identified in the same order in each of the synchronous image pairs to correctly match up the analogous corner points. These points, once corrected for optical distortion in individual cameras, were used to compute the epipolar geometry, by iteratively solving for the translation and rotation vectors that describe the relationship between the coordinate systems of the two cameras (Xu and Zhang, 1996). Once these matrices were estimated by the software, the three-dimensional position of a target point viewed in both cameras could be determined by triangulation.

Fish measurements with the camera

Fish lengths were measured by using stereo triangulation functions supplied with the camera calibration software package (Bouguet, 2008). For the video-drop system, images were extracted from the two video feeds at 1-s intervals. The images were synchronized at the beginning of each transect before deployment by using the LED synchronization light. The images were checked at the end of each transect to confirm that the cameras remained synchronized.

Length measurements were obtained by identifying the pixel coordinates of corresponding pixel locations in the left and right camera still frames such as a fish snout and tail (Fig. 3). These points were used to solve for the three-dimensional coordinates of the points in the images by triangulation, by using the calibration-derived parameters. Once the three-dimensional coordinates of the fish snout and tail were obtained, the length was measured as the simple Euclidian distance between the points in real space. This measurement method underestimated length for fish whose bodies were curved; however; fish in the video and still camera were almost exclusively seen with little or no curvature in their bodies and the few individuals that were obviously strongly curved were not measured. Length data were collected by using a basic software application built with the Matlab computing language (Fig. 4; available from the authors upon request), which incorporated the triangulation function supplied by the calibration toolbox.

In addition to length measurements, the three-dimensional coordinates extracted from the still-frame images provided data on the position and orientation of walleye Pollock in relation to the trawl (Fig. 5). These data were used to determine distances of pollock targets to trawl components for position of fish and to calculate tilt and yaw for orientation of fish.

Data collections

Field testing of the video-drop system was conducted 12–15 July 2008 at Zhemchug Ridges, located on the eastern Bering Sea shelf adjacent to Zhemchug Canyon where a sizable rockfish population is present in untrawlable and isolated rocky ridge area (Fig. 6; Rooper et al., in press). The camera system was deployed off the side of the vessel FV *Vesteraalen* by a winch suspended from a block attached to the vessel's crane. The camera sled drifted with the prevailing current, while the camera winch operator kept the seafloor in view and avoided any obstacles using real-time navigation. Stereo video was collected over 11 transects, each ranging in length from 3.5 to 49.5 min and covering distances of 95 m to 1673 m. Observations of trawl movements with the still-frame system were made during acoustic surveys of pollock in the eastern Bering Sea in June and July 2007 onboard the RV *Oscar Dyson* (Fig. 6).

Testing of the calibrations for the two camera systems

To test the video calibration five random still images was selected from the video-drop system of the checkerboard taken at the beginning and end of the study. Three intervals of 10 cm, 20 cm and 30 cm each were measured three times from the top to the bottom of the checkerboard (n=3 for each interval) and averaged within each frame. The average from each frame multiplied by the interval combination was then tested in an analysis of variance to determine whether there were significant differences between measurements from the first and second measurement set.

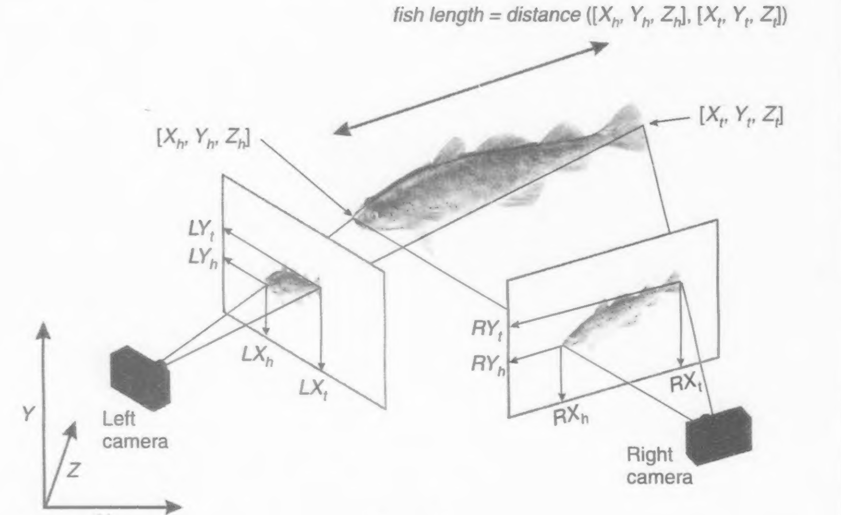


Figure 3

Method for determining fish length measurements by using stereo images. The three-dimensional coordinates of the fish head and tail (X_h, Y_h, Z_h; X_t, Y_t, Z_t) were determined by stereo-triangulation and by using the image-based coordinates from the image pairs (i.e., LX_h, LY_h; RX_h, RY_h). Fish length was estimated as the Euclidian distance between the three-dimensional points of the head and tail.

Results

Calibration

The estimates of distance of the fish to the trawl determined with the second calibration of the drop-video system were significantly larger and more variable than those from the first measurement set across all three intervals (Fig. 7). Differences between the mean measurements and known values in the second set ranged from 6.6% to 8.2%. However, the 95% confidence intervals for both sets included the actual values for the intervals in all cases, and the coefficients of variation for the measurements ranged to 5.5% of the mean value, indicating that the length measurements were reasonably precise. A similar procedure was also performed with the still-frame system, but only a single set of validation measurements was made before the start of field operations. The results of this set closely matched that of the first set made with the video cameras (Fig. 7).

Fish lengths determined with the video-drop system

The adult rockfish observed in the video were northern rockfish (96.94%), unidentified adult rockfish (*Sebastes* spp., 0.98%), adult Pacific ocean perch (0.49%), and dusky rockfish (*S. ciliatus*,1.60%), whereas most of the juveniles that were identified to species were Pacific ocean perch (Rooper et al. in press). Some of the juvenile rockfishes observed in the video were too small to identify to species. Individuals of each species group were randomly chosen to be measured in proportion with their abundance. Up to 200 randomly selected individual rockfish were measured in each transect, resulting in a total of 1489 length measurements. Rockfish were measured by using fork length only if both the tip of their snout and the end of the tail were plainly visible in both still images. If the randomly chosen rockfish could not be measured, the next available rockfish of the same species group that was deemed measureable was chosen. In a few cases, where the occurrence of a species group was very small (<5 individuals in a transect), none were measured.

A random sample of 20 rockfish that were observed in successive still frames of both video cameras was used to determine measurement precision and to estimate distance of the fish from the camera. These fish were measured in up to four consecutive frames and their estimated length were compared by using linear regression (Fig. 8). The percent difference between successive length measurements was not significantly related to the average fish length ($P=0.28$); in other words, there was no length-related bias in the measurements. The length data were also tested for a relationship with distance from the camera by using linear regression. There was no bias in the measurements of fish for distance from the camera ($P=0.29$). The standard deviation of

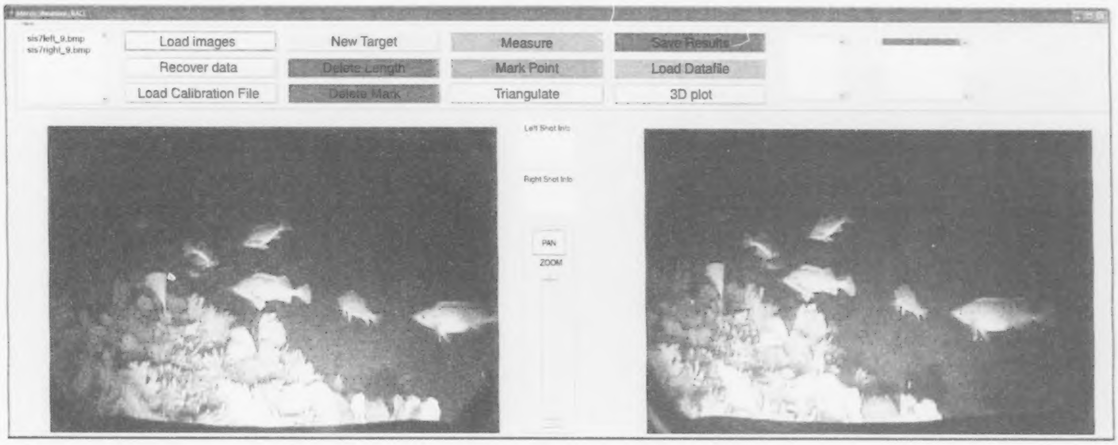


Figure 4

Computerized display of the stereo processing options for the drop stereo-video with a custom-built application written in the Matlab computing language. Synchronous images were extracted from videos taken by two cameras and used to estimate fish length. Images were taken in Zhemchug Ridges in the eastern Bering Sea in July 2008.

the percent difference in multiple measurements of the same fish was 0.076.

Analysis of still-frame stereo images

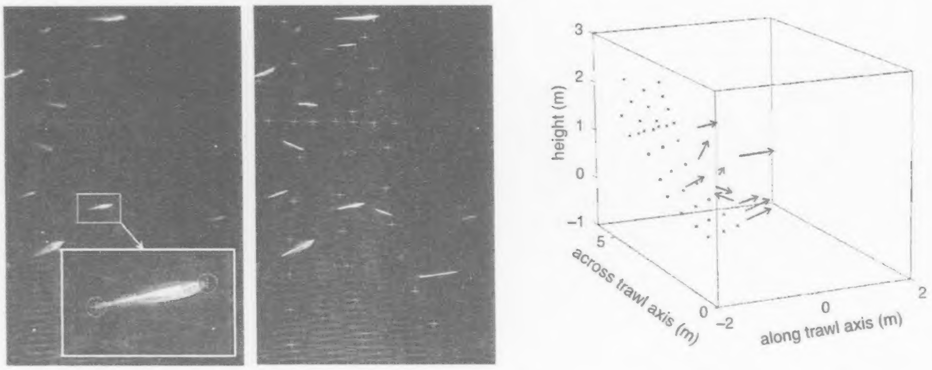
Ten deployments were made with the still-frame system, and ~200 fish were measured per deployment. Catches consisted almost exclusively of walleye pollock (>99%). A comparison between the length frequencies derived from the stereo analysis (n=360) and physical measurements of fish captured in the codend (n=1260, Fig. 9) showed that optical sampling approximates the length-frequency distribution of fish caught, despite the smaller sample size for optical sampling.

In addition to length measurements, the stereo analysis provided data on walleye pollock orientation and their relative position within the trawl. Quantitative descriptions of the distribution of tilt and yaw angles were easily calculated by using the same points in images (head and tail) derived for fish lengths (Fig. 10). To calculate the position of fish within the trawl additional corresponding points along the trawl panel were identified and their three-dimensional coordinates were determined by the triangulation process outlined above (Fig. 5).

Discussion

The potential of stereo cameras for measuring marine organisms has been shown in many studies (i.e., Shortis et al., 2000; Harvey et al., 2003), but here we present a description of the complete implementation of stereo cameras, including equipment costs (Table 1), image analysis process, and expected precision in data from these systems. The two stereo-camera systems described here were studied for their potential to provide information to augment fisheries assessment surveys in Alaska. Specifically, the stereo-camera systems in our study provided species and length data for untrawlable regions located within bottom-trawl survey boundaries and provide a new method for studying the behavior of fish in a midwater trawl. Our main goal was to present field-tested methods to provide quantifiable image-based data for fisheries surveys and our results may help similar research with stereo-camera–based sampling systems.

The video-drop system was useful for estimating rockfish size and species composition in field tests in Alaska. Error rates for size were on the order of 8.2% or less, which equates to about 2.5 cm for a 30-cm fish. Compared with other studies with error rates of ~0.1% to 0.7% in stereo-video systems (Harvey et al., 2002; Harvey et al., 2003; Shortis et al., 2009), the measurement error rate in our study was high. This rate represents systematic error most likely caused by the need to remove cameras from the housing after each deployment because a slight misalignment of the cameras in relation to the position at calibration would reduce the precision of the measurements. Ruff et al. (1995) report an achievable level of precision in measuring fish of 3.5%, based on repeat measurements of individuals, which is also better than the 5.9% observed in our study. The error rates also compare well to the rates of 1–5% for measuring rigid items with parallel lasers (Rochet et al., 2006). However, only fish on or near which the parallel laser beams are projected can be measured. This restriction limits the measurement sample size. In contrast, any fish simultaneously viewed by both cameras in a stereo-camera system can be mea-



A raw image **B** processed image **C** 3D reconstruction

Figure 5

Images of walleye pollock (*Theragra chalcogramma*) from a still-frame stereo camera in a midwater trawl and a 3-D reconstruction of fish in relation to the trawl net. (**A**) Fish lengths were measured by enlarging the image of a fish and indicating the position of the snout and tail (shown as U) in both right and left raw images (only the left image is shown above). (**B**) The chosen fish endpoints are overlaid on the image as lines. In addition to estimates of fish length, stereo-processing allows the position of fish in relation to the trawl to be estimated. Additional points in the images can be determined by finding corresponding left-right image pixel coordinates (B, shown as crosses). (**C**) Following stereo-triangulation, a three-dimensional plot shows the fish targets as arrows and trawl mesh knots as dots.

sured, and thus the number of fish that can be measured is larger from the same length transect. Improvements in the quality of the still-frame images and in the collection of calibration data from a target at the beginning of each transect may allow more precise measurements to be taken in future studies. Given our inability with other survey gears to determine fish size and species composition in untrawlable habitats, the use of stereo cameras holds promise for stock assessments of rockfish and other species. Stereo-camera-based sampling could also be used broadly wherever gears other than bottom trawls are needed to obtain species- or size-composition information.

Lengths of rockfish derived from the video-drop system were generally comparable to trawl catch-based size distributions for the species exam-

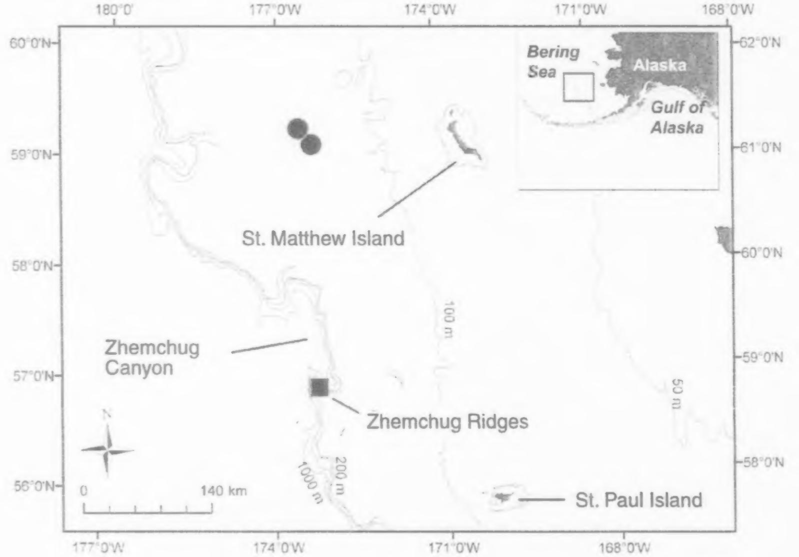

180°0'
177°0'W
174°0'W
171°0'W
168°0'W
60°0'N
59°0'N
58°0'N
57°0'N
56°0'N
62°0'N
61°0'N
60°0'N
59°0'N
58°0'N
Bering Sea
Alaska
Gulf of Alaska
St. Matthew Island
100 m
Zhemchug Canyon
Zhemchug Ridges
50 m
N
0
140 km
200 m
1000 m
St. Paul Island
177°0'W
174°0'W
171°0'W
168°0'W

Figure 6

Map of study areas in the eastern Bering Sea showing the location of field tests of the drop stereo video cameras for sampling untrawlable areas (black square) in July 2008 and for sampling fish behavior in a trawl (circles) with a still-frame stereo camera in July 2007.

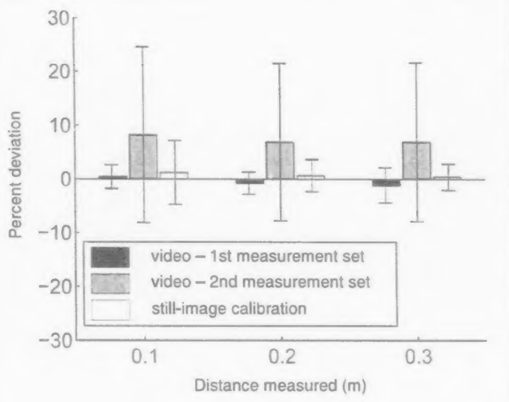


Figure 7

Results of measuring known distances on the checkerboard (see Fig. 2) during the first and second calibrations of the drop stereo video-camera system and a still-frame stereo-camera system used for estimating fish length and studying behavior. Calibration is a necessary step in the use of stereo cameras to allow measurements to be made from images. Values represent the percent deviation in measurements in relation to known values, including 95% confidence intervals based on five measurements.

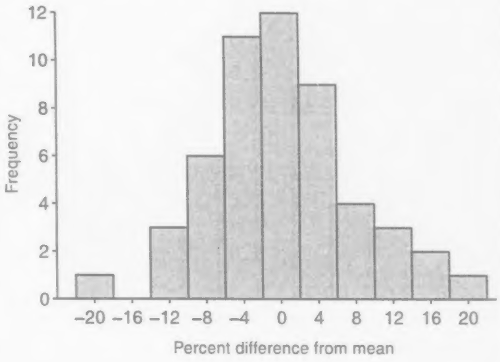


Figure 8

Frequency of percent differences from multiple length measurements of $n=20$ rockfish and the mean length of the fish. Individual fish were measured multiple times from a series of images extracted from video taken by a drop stereo-video camera. Measurements from each image were then compared to the mean measurement for that individual to estimate potential measurement error. Rockfish observations were collected at Zhemchug Ridges, eastern Bering Sea in July 2008.

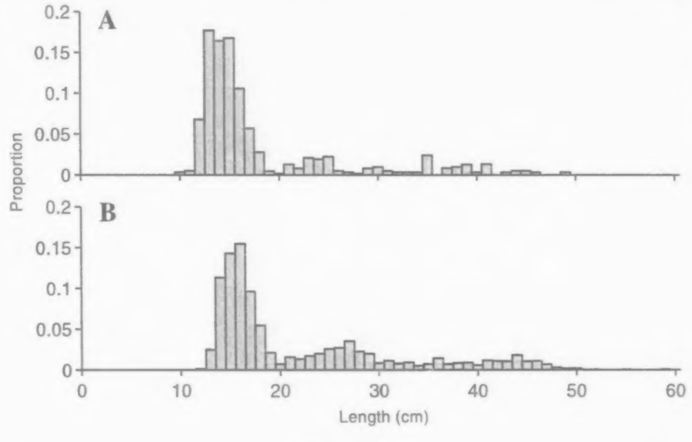


Figure 9

Comparison between length frequencies of walleye pollock (*Theragra chalcogramma*) estimated from (**A**) the images from a still-frame stereo camera ($n=360$) within a midwater trawl, and length frequencies obtained from (**B**) fish captured in the codend and directly measured ($n=1260$). The smaller camera-based sample results are similar to the direct measurements in their overall size distribution, but there was less definition for larger fish (>20 cm). Data were pooled from three trawl samples taken in the eastern Bering Sea in July 2007.

ined. Northern rockfish lengths from stereo-video images taken along transects at Zhemchug Ridges ranged from 9 to 41 cm (mean length=30.0 cm). In three bottom-trawl surveys near the Aleutian Islands, Clausen and Heifetz (2002) found that the mean size of northern rockfish was 29.9 cm and ranged from 15 to 38 cm. Juvenile Pacific ocean perch lengths (2.6 cm to 25.0 cm) were similar but ranged to smaller sizes than those found for the Aleutian Islands (8.3cm to 24.9 cm; Boldt and Rooper, 2009). Lengths of juvenile Pacific ocean perch obtained from stereo video were also similar to those in three experimental tows in the Zhemchug Ridges area in 2004 and 2007 (juveniles ranged from 10 cm to 25 cm). However, these lengths were measured from fish captured during bottom trawl hauls, where the incidence of smaller fish may have been due to reduced catchability of smaller individuals. Although these observations are not meant to serve as a quantitative comparison of trawl- and stereo-camera–derived size estimates, they demonstrate the similarities in information supplied by the two methods and the potential for stereo cameras to overcome some problems with the catchability of juvenile fish.

The stereo camera was very useful for studying behavior of pollock in the trawl. The data show the possibility of performing a length-based analysis of behavior which will directly contribute to studies of gear selectivity and future designs of scientific trawl gear. Although a postsurvey calibration was not performed with the still-frame system, the cameras were securely fastened in the housings and were not removed during the entire data collection, thus maintaining intercamera spacing and angles. The agreement between the catch-based length measurements and the stereo-derived lengths provides direct validation of the stereo-derived measurements. The low sampling frequency of 1 frame per 5 s ensured minimal influence of the artificial lighting from the cameras on behavior because the fish photographed had not been previously exposed to the light source.

Recent development of high-resolution digital imaging devices and an increased access to custom designed, freely available software tools have made stereo-camera methods easy to implement by research groups without direct expertise in the subject. The camera calibration toolbox (Bouguet, 2008) provided the basis for software development. Although the current analysis approach is still fairly time intensive, the volumes of data analyzed were not very large. In a routine application of stereo-video cameras in untrawlable areas, additional levels of automated processing would likely be required because the quantity of video footage would substantial. For some aspects of the analysis, such as the matching of targets on the stereo cameras and the extraction of fish lengths, automation may be attainable, whereas automating more difficult tasks of isolating and identifying fish targets may not be feasible.

Stereo photography will continue to be developed as survey tools are developed for monitoring fish stocks and thereby improving the quality of stock assessments of fishery resources in Alaska. Some challenges remain; for instance, the challenge of institutionalizing image-based sampling as a routine survey method for untrawlable habitats. As a method of studying fish behavior in trawls, stereo cameras provide promising results by allowing three-dimensional reconstructions of the trawl environment.

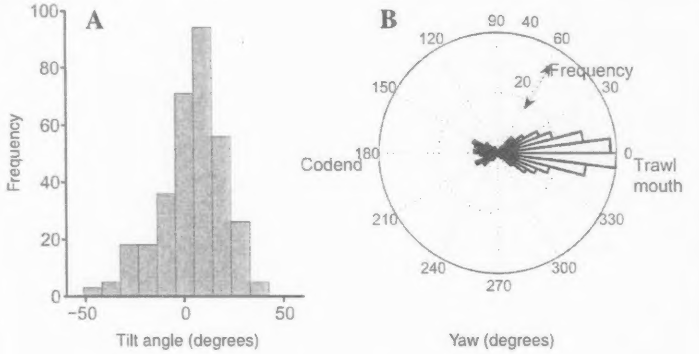


Figure 10

Orientiation of walleye pollock (*Theragra chalcogramma*) within a midwater trawl. A still-frame stereo camera was used to determine (**A**) the distribution of individual fish tilt angle (deviation of snout-tail axis from the horizontal), and (**B**) the yaw (angle of fish heading in the horizontal plane). Most fish were oriented horizontally and facing toward the trawl opening. Image data were collected in the eastern Bering Sea in July 2007 as part of a study of fish behavior within the trawl.

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2003. Calculation of untrawlable areas within the boundaries of a bottom trawl survey. Can. J. Fish. Aquat. Sci. 60:657–669.

Best paper awards for 2009

The award for best publication of the year is given to authors who are employees of the National Marine Fisheries Service, NOAA, and whose articles are judged to be the most noteworthy of those published in *Fishery Bulletin* and *Marine Fisheries Review*. Authors from the National Marine Fisheries Service are noted in bold below.

The winners for *Fishery Bulletin*:

First prize:
Jeffrey J. Polovina, Melanie Abecassis,
Evan A. Howell, and Phoebe Woodworth

Increases in the relative abundance of mid-trophic level fishes concurrent with declines in apex predators in the subtropical North Pacific, 1996–2006.
Fish. Bull. 107:523–531.

Honorable mention:
Richard Brill, Peter Bushnell, Leonie Smith, Coley Speaks, Rumya Sundaram, Eric Stroud, and John Wang

The repulsive and feeding-deterrent effects of electropositive metals on juvenile sandbar sharks (*Carcharhinus plumbeus*).
Fish. Bull. 107:298–307.

The winners for *Marine Fisheries Review*:

Phil Clapham and Yulia Ivashchenko.
A Whale of a Deception

This article documents the untold numbers of whales taken by the Soviet whaling industry in violation of international quotas. The article was discussed in the "News of the Week" section of the journal *Science*: "Mystery of the Missing Humpbacks Solved by Soviet Data." Science, vol. 324:1132. May 29, 2009.
Mar. Fish. Rev. 71(1):44–52.

Fishery Bulletin

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